CALCAREOUS FEN VEGETATION AND ECOLOGY

AND THE DISJUNCT *BETULA GLANDULOSA*

IN SOUTHEASTERN ALASKA

By

Joni M. Johnson

RECOMMENDED:

Advisory Committee Chair

Assistant Chair, Department of Wildlife and Biology

APPROVED:

Dean, College of Natural Science and Mathematics

Dean of the Graduate School

July 26, 2006

Date

CALCAREOUS FEN VEGETATION AND ECOLOGY AND THE DISJUNCT *BETULA GLANDULOSA* IN SOUTHEASTERN ALASKA

A

THESIS

Presented to the Faculty

of the University of Alaska Fairbanks

in Partial Fulfillment of the Requirements

for the Degree of

MASTER OF SCIENCE

By

Joni M. Johnson

Fairbanks, Alaska

August 2006

Abstract

Calcareous fens are rare within southeastern Alaska due to their unique geochemical setting, as are the plant communities produced by these environs. On a global scale these wetland types have been identified as valuable for their biodiversity and have received special protection. The first objective of this research was to characterize the floristics and hydrogeochemistry of a subset of calcareous fens on Chichagof Island in the northern Alexander Archipelago through intensive sampling within each site. Multivariate analyses were used to describe these wetland systems. The second objective of this study included investigating whether or not the disjunct *Betula glandulosa* (dwarf birch) population was restricted to its current site. *B. glandulosa* is a habitat generalist in its known range; however, it is found in only one location within the Alexander Archipelago. Germination and seedling transplant experiments were conducted that tested for the effects of site, competition, and the interaction between site and competition. In this manner a subset of calcareous fens in the region was described and abiotic parameters associated with *B. glandulosa* evaluated. Obtaining baseline information and understanding mechanisms behind these sources of regional biodiversity are important for monitoring purposes and detecting disturbance effects.

Table of Contents

Page

List of Figures

Page

List of Tables

Page

Acknowledgements

This work was supported in part by the USDA Forest Service, the Pacific Northwest Research Station Forest Sciences Laboratory, the Center for Global Change and the U.S. Fish and Wildlife Service. Dave D'Amore's enthusiasm and assistance with water sample analysis were much appreciated, as was the help in the field from Eric Johnson, Karen Dillman and Eric Bloechle. This thesis was improved with valuable editing by Christa Mulder.

GENERAL INTRODUCTION

Calcareous fens within southeastern Alaska are uncommon due to the scattered presence of limestone geology. Wetlands characterized as calcareous fens are considered to be one of the rarest wetland types in North America, and throughout the world these fens are associated with rare and sensitive plant species as well as high biodiversity (Almendinger and Leete 1998b, MDNR 1995, Boyer and Wheeler 1989). Globally, these wetland types are the target of conservation measures due to their floristic and faunal diversity and their support of rare and uncommon species. Within southeastern Alaska, the unique plant communities present in calcareous fens are recognized for containing high species diversity, as well as including peripheral or disjunct species (McClellan et al. 2003). These uncommon wetland types are frequently found within watersheds that are heavily managed for timber harvest, hence the need to describe these systems in southeastern Alaska as well as provide baseline data for future monitoring. Aside from a cursory sampling of water chemistry and a gross floristic survey (McClellan et al. 2003), no known research has occurred within calcareous fens in the region.

Alexander Archipelago and the study sites

The Alexander Archipelago in southeastern Alaska consists of approximately one thousand islands adjacent to the mainland Coastal Mountains. The region is a perhumid rainforest with mild winters and cool summers (Alaback 1996). Mean temperatures at sea level are 10°C in the summer and 0°C in the winter, and mean annual rainfall is 254 cm (Nowacki et al. 2001). Wetlands in the Tongass National Forest compose 30 percent of the land base (USDA 1997), of which only a small fraction are calcareous fens. The two study sites are located in the Game Creek watershed on northeastern Chichagof Island, in the northern region of the archipelago. This area consists of a mix of carbonate and non-carbonate sedimentary rock as well as scattered volcanic and intrusive igneous rocks (Karl 1996, Nowacki et al. 2001).

The two research sites selected for study were shrub fens two kilometers apart within the same watershed, both of which fall within the discharge zone of the Kennel Creek limestone formation. These two sites differ primarily in the presence or absence of *B. glandulosa*. The site with *B. glandulosa* houses the only known population within the Alexander Archipelago, disjunct from the known mainland distribution on the other side of the Coastal Mountain Range. The sites are roughly 100 m above sea level, located at the base of a massive limestone ridge. Terracing occurs in both sites, likely the result of down-cutting over time from the tributary at the base of the slope.

Fen classification

Wetland classification broadly separates peatlands into ombrotrophic (rainwater fed) and minerotrophic (groundwater fed) wetlands (Mitsch and Gosselink 2000, National Wetlands Working Group 1988). Fens are minerotrophic, distinguished from ombrotrophic bogs and surface water-fed wetlands by their groundwater source. The classification terminology varies widely for fens, with characterization of wetlands based on water source, water chemistry, vegetation (e.g., Cowardin et al. 1979), or substrate. This variation in terminology reflects the complexity as well as the biotic and abiotic continuum that exists within wetland systems. Authors select different divisions along these gradients for descriptive purposes; therefore, the classification schemes are somewhat arbitrary. Moreover, regional and continental traditions contribute to this variation, as a single term could apply to different wetland types in Europe as opposed to Canada.

The majority of wetland descriptive studies classify peatlands using a limited number of geochemical parameters, namely pH, conductivity and calcium. This classification looks for divisions along a chemical gradient as indicated by vegetation composition. In 1949 Du Rietz formalized classification of wetland types based on water chemistry and vegetation indicators

(National Wetlands Working Group 1988). Sjörs (1950, 1969) modified this classification scheme by determining the water chemistry that separates bogs from fens, and then further dividing fens into poor, intermediate, and rich classes using both water chemistry and vegetation composition. The Sjörs classification system has been further refined, dividing fens into very poor, moderately poor, intermediate, moderately rich, and rich classes (e.g., Foster and King 1984, Chee and Vitt 1989), again on the basis of water chemistry and vegetation. Moore and Bellamy (1974) classified fens into three types based on water chemistry alone: weakly minerotrophic, moderately minerotrophic, and strongly minerotrophic. The pH is sometimes used as a surrogate for a poor to rich gradient in nutrient availability within wetland systems; the lower pH is at the poor fen end of the spectrum whereas the higher pH would be considered a rich fen (Bedford and Godwin 2003). Out of the numerous gradients that occur within wetlands and within classifications, the poor to rich spectrum refers to the richness of indicator species for high base cation content and should not be confused with nutrient availability (Bedford and Godwin 2003, Bridgham et al. 1996, Slack et al. 1980, Wheeler and Proctor 2000). The multiple terms used for multiple descriptive gradients caused Bridgham et al. (1996) to recommend using "bogs" or "fens" to describe the different peatlands and avoid the confusion caused by existing terminology.

Calcareous fens

More specific terminology has been used by botanists, ecologists, hydrologists, and soil scientists to describe types of fens, such as calcareous fen, marl fen, and prairie fen. The term calcareous fen is often used interchangeably with rich fen, describing wetlands that have calcium-rich groundwater inputs, hydric soils, calciphilic vegetation, and circumneutral to alkaline pH (Almendinger and Leete 1998a, Bedford and Godwin 2003). Oftentimes marl or tufa is found in these systems from glacial sediment or lacustrine deposition, and marl or tufa can be formed

through the accumulation of carbonate over time (Amon et al. 2002, Almendinger and Leete 1998a). Calcareous fens are located within the hydrologic discharge zone at the base of limestone outcroppings and ridges, or where wetland groundwater sources are in contact with carbonate lithology (Almendinger and Leete 1998b, McClellan et al. 2003). The resulting hydrogeochemistry is distinct from the predominant bog and fen communities of the surrounding area, and within southeastern Alaska each island has unique species present within these calcareous fen complexes (McClellan et al. 2003). Only a few calcareous fens have been described within Alaska and British Columbia either for classification purposes (MacKenzie and Moran 2004, Racine and Walters 1994) or to assess whether or not calcareous fens as defined by the Minnesota Department of Natural Resources (1995) were present (McClellan et al. 2003,).

The vegetation of calcareous fens has been described in other regions of North America as well, including Colorado (Johnson and Steingraeber 2003), the Midwest (Almendinger and Leete 1998b, Bowles et al. 2005, Glaser 1990, Komor 1994, Reed 1985), New England (Motzkin 1994, Picking and Veneman 2004, Van Hoewyk et al. 2000), and Alberta, Canada (Slack et al. 1980, Chee and Vitt 1989, Vitt and Chee 1990). Across the continent, these studies have documented rare plant species and disjunct plant populations within calcareous fens. In Colorado, several species are disjuncts from the circumboreal floristic province while 15 state rare or endemic plants have been identified (Cooper 1996, Johnson and Steingraeber 2003); in Iowa some 80 species identified in calcareous fens are disjunct from their circumboreal distribution (Bedford and Godwin 2003, Nekola 1994); and in Idaho, 35 uncommon or rare taxa have been identified in calcareous fens (Chadde et al. 1998).

Vegetation patterns and environmental gradients

Hydrology, conductivity, pH, and mineral and nutrient concentrations are well-known underlying gradients influencing vegetation patterns in wetlands systems (Bedford et al. 1999, Bridgham et al. 1996, Slack et al. 1980, Vitt and Chee 1990). In studies that focus on water chemistry when describing plant communities within calcareous fens (Motzkin 1994, Komor 1994, Chee and Vitt 1989, Slack et al. 1980), pH, conductivity, and calcium concentrations have been related to different vegetation types. Teasing apart the relationship of water chemistry to species composition from the influence of the hydrological fluctuations on ionic fluxes creates a difficulty. The water table is the predominant gradient influencing species composition in several of the fens studied (Johnson and Steingraeber 2003, Picking 2002, Slack et al. 1980). The water discharging into the system is important in maintaining these plant communities, yet the absence of underlying chemical gradients suggests that the high temporal and spatial variation of water chemistry may not be as strong of a factor influencing species composition as the substrate. Alternatively, the absence of water chemistry gradients may be an artifact of water sampling challenges due to the variability of the spatial flow of water as well as the sensitivity of water to precipitation and evaporation.

A handful of descriptive papers include the substrate in the classification of calcareous wetland plant communities. For Midwestern fen systems, the lack of gradients corresponding with vegetation assemblages has been attributed to the focus on water chemistry (Amon et al. 2002, Bowles et al. 2005). Multivariate analyses of the soil substrate and floristics within one particular site described substantive gradients in organic content and cation exchange capacity as well as pH and base cation gradients that corresponded with plant community types (Bowles et al. 2005). These findings have been replicated in other studies that include the substrate in the sampling (Vitt and Chee 1990, Motzkin 1994).

Disjunct populations

Disjunct plant populations are distant from continuous populations within the geographical range of the species. Disjunctions can occur at different geographical scales, from smaller scales such as found in the European Alps (Schonswetter et al. 2003) to larger like those found with some Beringean species (Murray et al. 1983). Generally, there are two types of disjunctions: disjunctions that result in speciation events are "specific disjunctions," whereas disjunctions that do not produce speciation events are "intraspecific disjunctions." Plant disjunctions are of interest for a number of reasons. Specific disjunctions provide opportunities for study of speciation events that result from adapting to different environs (Brown and Lomolino 1998). Intraspecific disjunctions can result from historical factors such as glaciation events, and thus provide information for retracing climatic events as well as the dispersal of species (Strong and Hills 2003). Intraspecific disjunctions may also result from long-distance chance dispersal or introduction by humans where taxon persistence is linked to some key ecological factor.

Within the Alexander Archipelago of southeastern Alaska, the Coastal Mountain Range and the Pacific Ocean create barriers to species' dispersal. The northern region is known to house peripheral taxa at the southern limit of their known range where unusual substrates are present (e.g., limestone and ultramafic geology). Likewise, peripheral species at the northern limit of their known range are present in the southern region of southeastern Alaska. Calcareous fens provide unique environmental conditions, and populations on the fringe of their known range have been identified in these systems within southeastern Alaska (McClellan et al. 2003). Few plants are endemic, and most rare plants are shared with the Canadian and Vancouverian floristic provinces. The glacial history of the region strongly influences the present-day landscape.

***B. glandulosa* origin**

B. glandulosa could have become established within the Game Creek watershed through human introduction or long-distance chance dispersal events. I obtained a *B. glandulosa* sample from 50-cm depth in the Game Creek site in 2004, the radiocarbon date placing the shrub in this locale at least 250 BP. This eliminates the possibility of recent anthropogenic introduction; however, Huna Tlingit have lived and traded in the area for at least 250 years (Howell et al. 2005). Prehistoric villages in the vicinity date 8,500 BP (Goldschmidt and Haas 1998) and are located on the opposite side of the mountain pass from the closest documented population in the St. Elias Mountains. The opening of mainland rivers after the last glacial maxima provides possible corridors for long-distance chance dispersal from the interior. Wind is the predominant mechanism for seed dispersal; however, the large seed size (3-4 mm) is not well adapted for long-distance transport. Furthermore, if De Groot (1997) was correct and seeds disperse in the fall, the heavy rainfall may dampen long distance transport. If, on the other hand, the seeds persist over the winter (Viereck and Little 1986), then seed may disperse in March and April, typically the driest months of the year in this region.

During the Late-Wisconsin glacial maximum in southeastern Alaska, refugia existed on nunataks as well as in scattered coastal locations on the outer islands and mainland around Lituya Bay (Carrara et al. 2002, Worley 1980). Pollen records indicate that herbaceous plants were the first to recolonize, followed by alder (Heusser 1989) and then trees roughly 8,000 BP (Cwynar 1990, Heusser 1952, Mann and Hamilton 1995). These records do not document *B. glandulosa* in any of the cores sampled, which is not to say that the species did not persist in refugia or in the seed bank, but that the probability is very low. Elsewhere in North America, paleopalynology works indicate that *B. glandulosa* was most abundant at the onset and at the end of the cooler Lower Dryas circa 12,500-10,000 BP, with peak abundance following the onset of cooler

temperatures by an estimated 80 years (De Groot et al. 1997, Mayle and Cwynar 1995, Watts 1979). This lag in *B. glandulosa* dominance indicates that biotic or soil abiotic factors controlled presence more than some inherent response of the taxon to climate change. As temperature increased following the last glacial maximum, *B. glandulosa* abundance decreased.

Ecological sensitivity

Gilvear et al. (1993) noted that shifts in plant community composition of calcareous fens may result from small changes in the groundwater/precipitation/surface water balance, and it is widely recognized that hydrology plays a dominant role in shaping wetland soil genesis and vegetation distribution (Eser and Rosen 1999). There is a need for baseline knowledge of wetland hydrogeological function and the ecological conditions of calcareous fens within the region to better predict wetland response to disturbance. The very notion that disjunct species may be useful indicators of change within their habitat -- as they are found outside their normal range in stressful environments or in small patches of suitable habitat (Lennon et al. 2002) -- underscores the import of wetland function in maintaining regional biodiversity.

Study objectives

Two sites were selected for study due to the presence of disjunct and peripheral species as well as in the unique geochemical setting. To study the occurrence of the disjunct *Betula glandulosa* Michx., known from only one site within the Alexander Archipelago, a second site was selected that appeared similar in all aspects but the presence of *B. glandulosa*. In this manner a subset of calcareous fens in the region was described and abiotic parameters associated with *B. glandulosa* evaluated. The objectives of this project were twofold:

a) Complete a detailed floristic analysis and quantify the hydrological and geochemical conditions related to species composition within two calcareous fens in the region, one of which houses the disjunct species *B. glandulosa*.

b) Assess whether or not the disjunct *B. glandulosa* population is restricted to its current site by evaluating two life stages of *B. glandulosa*.

The studies addressing each of these objectives are presented in Chapter 1 and Chapter 2. The introduction provides a brief description of the research area and presents a general literature review. New questions and directions for future research are presented in the general conclusion.

REFERENCES

Alaback, P. B. 1996. Biodiversity pattern in relation to climate: the Coastal Temperate Rainforests of North America. In High-latitude rainforests and associated ecosystems of the West Coast of the Americas. R.G. Lawford, P.B. Alaback and E. Fuentes eds. Springer-Verlag, Inc., New York, NY, USA.

Almendinger, J. E. and J. H. Leete. 1998a. Peat characteristics and groundwater geochemistry of calcareous fens in the Minnesota River Basin, U.S.A. Biogeochemistry 43:17-41.

Almendinger, J. E. and J. H. Leete. 1998b. Regional and local hydrogeology of calcareous fens in the Minnesota River Basin, USA. Wetlands 18:184-202.

Amon, J. P., C. A. Thompson, Q.J. Carpenter and J. Miner. 2002. Temperate zone fens of the glaciated Midwestern USA. Wetlands 22:301-317.

Bedford, B. L. and K. S. Godwin. 2003. Fens of the United States: Distribution, characteristics, and scientific connection versus legal isolation. Wetlands 23:608-629.

Bedford, B. L., M. R. Walbridge and A. Aldous. 1999. Patterns in nutrient availability and plant diversity of temperate North American wetlands. Ecology 80:2151-2169.

Bowles, M. L., P. D. Kelsey and J. L. McBride. 2005. Relationships among environmental factors, vegetation zones, and species richness in a North American calcareous prairie fen. Wetlands 25:685-696.

Boyer, M. L. H. and W. D. Wheeler. 1989. Vegetation patterns in spring-fed calcareous fens: Calcite precipitation and constraints on fertility. Journal of Ecology 77:597-609.

Bridgham, S. D., J. Pastor, J. A. Janssens, C. Chapin and T. J. Malterer. 1996. Multiple limiting gradients in peatlands: A call for a new paradigm. Wetlands 16:45-65.

Brown, J. H. and M. V. Lomolino. 1998. *Biogeography*, 2nd ed. Sinauer Associates, Sunderland, MA.

Carrara, P. E., T. A. Ager, J. F. Baichtal and D. Van Sistine. 2002. Late Wisconsin glacial limits in southern southeastern Alaska, as indicated by a new bathymetric map. Abstracts for Institute of Arctic and Alpine Research, University of Colorado, Boulder, CO, USA.

Chadde, S. W., J. S. Shelly, R. J. Bursik, R. K. Moseley, A. G. Evenden, M. Mantas, F. Rabe and B. Heidel. 1998. Peatlands on National Forests of the Northern Rocky Mountains: Ecology and Conservation. General Technical Report RMRS-GTR-11. U.S. Forest Service, Rocky Mountain Research Station, Ogden, UT, USA.

Chee, W. and D. H. Vitt. 1989. The vegetation, surface chemistry, and peat chemistry of moderate-rich fens in Central Alberta, Canada. Wetlands, 9:227-261.

Cooper, D. J. 1996. Water and soil chemistry, floristics and phytosociology of the extreme rich High Creek fen, in South Park, Colorado, U.S.A. Canadian Journal of Botany 74:1801-1811.

Cowardin, L. M., V. Carter, F. C. Golet and E. T. Laroe. 1979. Classification of wetlands and deepwater habitats of the United States. Report No. FWS/OBS-79/31. United States Department of the Interior Fish and Wildlife Service, Washington, DC, USA.

Cwynar, L. C. 1990. A late Quaternary vegetation history for Lily Lake, Chilkat Peninsula, southeast Alaska. Canadian Journal of Botany 68:1106-1112.

De Groot, W. J., P. A. Thomas and R.W. Wein. 1997. *Betula nana* L. and *Betula glandulosa* Michx. Journal of Ecology 85:241-264.

Eser, P. and M.R. Rosen. 1999. The influence of groundwater hydrology and stratigraphy on the hydrochemistry of Stump Bay, South Taupo Wetlands, New Zealand. Journal of Hydrology 220:27-47.

Foster, D. R. and G. A. King. 1984. Landscape features, vegetation and developmental history of a patterned fen in southeastern Labrador, Canada. Journal of Ecology 72:115-143.

Gilvear, D. J., R. Andrews, J. H. Tellam, J. W. Lloyd and D. N Lerner. 1993. Journal of Hydrology 144:311-334.

Glaser, P. H., J. A. Janssens and D. I. Siegel. 1990. The response of vegetation to chemical and hydrological gradients in the Lost River Peatland, northern Minnesota. Journal of Ecology 78:1021-1048.

Goldschmidt, W. R. and T. H. Haas. 1998. *Haa Aani: Our Land.* University of Washington Press, Seattle, WA, USA.

Heusser, C. J. 1952. Pollen profiles from southeastern Alaska. Ecological Monographs 22:331-352.

Heusser, C. J. 1989. North Pacific coastal refugia - the Queen Charlotte Islands in perspective. *In* Scudder, G.G.E. and Gessler, N., (eds.). The Outer Shores, proceedings of the Queen Charlotte Islands 1st International Symposium, University of British Columbia, August, 1984. Queen Charlotte Islands Museum Press, Skidegate, B.C.

Howell, W., D. Monteith, C. Connor and G. Streveler. 2005. Huna Tlingit responses to rapid glacial advance and retreat in Glacier Bay. Proceedings Rapid Landscape Change in the Arctic and sub-Arctic, Whitehorse, Yukon, Canada.

Johnson, J. B. and D. A. Steingraeber. 2003. The vegetation and ecological gradients of calcareous mires in the South Park valley, Colorado. Canadian Journal of Botany 81:201-219.

Karl, S. 1996. Preliminary geologic map of northeastern Chichagof Island, Alaska. Open File report 96-53. U.S. Geological Service, Denver, CO, USA.

Komor, S. C. 1994. Geochemistry and hydrology of a calcareous fen within the Savage Fen wetlands complex, Minnesota, USA. Geochimica et Cosmochimica Acta 58:3353-3367.

Lennon, J. L., W. E. Kunin, S. Corne, S. Carver and W. W. S. Van Hees. 2002. Are Alaskan trees found in locally more favourable sites in marginal areas? Global Ecology and Biogeography 11:103-114.

MacKenzie, W. H. and J. R. Moran. 2004. Wetlands of British Columbia: a guide to identification. Land Management Handbook No. 52. Research Branch, British Columbia Ministry of Forestry, Victoria, B.C., Canada.

Mann, D. H. and Hamilton, T. D., 1995, Late Pleistocene and Holocene paleoenvironments of the north Pacific coast. Quaternary Science Reviews, v. 14, p. 449-471.

Mayle, F. E. and L. C. Cwynar. 1995. Impact of the Younger Dryas cooling event upon lowland vegetation of maritime Canada. Ecological Monographs 65:129-154.

McClellan, M. H., T. Brock and J. F. Baichtal. 2003. Calcareous fens in southeast Alaska. PNW-RN-536. USDA Forest Service Pacific Northwest Research Station, Juneau, AK, USA.

Minnesota Department of Natural Resources (MDNR). 1995. Technical criteria for identifying and delineating calcareous fens in Minnesota. Minnesota Department of Natural Resources, St. Paul, MN, USA.

Mitsch, W. J. and J. G. Gosselink. 2000. *Wetlands*. 3rd ed. John Wiley & Sons, Inc., New York, NY, USA.

Moore, P. D. and D. J. Bellamy. 1974. *Peatlands: A guide to marshes and shallow open water wetlands in the grasslands and parklands of the prairie provinces*. Springer-Verlag, New York, New York, USA.

Motzin, G. 1994. Calcareous fens of western New England and adjacent New York State. Rhodora 96:44-68.

Murray, D. F., B. M. Murray, B. A. Yurtsev and R. Howenstein. 1983. Biogeographic significance of steppe vegetation in subarctic Alaska. Permafrost: Fourth International Conference, Proceedings 4:883-888.

National Wetlands Working Group. 1988. *Wetlands of Canada*. Ecological Land Classification Series No. 24. Sustainable Development Branch, Environment Canada, Ottawa, Ontario and Polyscience Publications, Inc., Montreal, Quebec, Canada.

Nekola, J. C. 1994. The environmental and vascular flora of northeastern Iowa fen communities. Rhodora 96:44-68.

Nowacki, G., M. Shephard, P. Krosse, W. Pawuk, G. Fisher, J. Baichtal, D. Brew and E. Kissinger. 2001. Ecological Subsections of Southeast Alaska and Neighboring Areas of Canada. R10-TP-75. USDA Forest Service, Alaska Region, Anchorage, AK, USA.

Picking, D. J. 2002. Vegetation patterns and associated hydrogeochemical cycles in a calcareous sloping fen of southwestern Massachusetts. Ph.D. Dissertation. University of Massachusetts, Amherst, MA, USA.

Picking, D. J. and P. L. M. Veneman. 2004. Vegetation patterns in a calcareous sloping fen of southwestern Massachusetts, USA. Wetlands 24:514-528.

Racine, C. H. and J. C. Walters. 1994. Groundwater-discharge fens in the Tanana Lowlands, Interior Alaska, U.S.A. Arctic and Alpine Research 26:418-426.

Reed, D. M. 1985. Composition and distribution of calcareous fens in relation to environmental conditions in southeastern Wisconsin. MS. Thesis, University of Wisconsin-Milwaukee, WI, USA.

Schonswetter, P. A. Tribsch, G. M Schneeweiss and H. Niklfeld. 2003. Disjunctions in relict alpine plants: phylogeography of *Androsace brevis* and *A. wulfeniana* (Primulaceae). Botanical Journal of the Linnean Society 141:437-446.

Sjörs, H. 1950. On the relation between vegetation and electrolytes in north Swedish mire waters. Oikos 2:241-258.

Sjörs, H. 1969. Bogs and fens in the Hudson Bay Lowlands. Arctic 12:3-19.

Slack, N. G., D. G. Vitt and D. G. Horton. 1980. Vegetation gradients of minerotrophically rich fens in western Alberta. Canadian Journal of Botany 58:330-350.

Strong, W. L. and L. V. Hills. 2003. Post-hypsithermal plant disjunctions in western Alberta, Canada. Journal of Biogeography 30:419-430.

USDA. 1997. Tongass National Forest Land and Resource Management Plan. R10-MB-338dd. USDA Forest Service Region 10, Juneau, AK, USA.

Van Hoewyk, D., P. M. Groffman, E. Kivita, G. Mihocko and G. Stevens. 2000. Soil nitrogen dynamics in organic and mineral soil calcareous wetlands in eastern New York. Soil Sciences of America Journal 65:2168-2173.

Viereck, L.A. and E. L. Little, Jr. 1986. Alaska Trees and Shrubs. University of Alaska Press: Fairbanks. pp. 130-132.

Vitt, D. H. and W. H. Chee. 1990. The relationships of vegetation to surface water chemistry and peat chemistry in fens of Alberta, Canada. Vegetatio 89:87-106.

Watts, W. A. 1979. Late quaternary vegetation of central Appalachia and the New Jersey coastal plain. Ecological Monographs 49:427-469.

Wheeler, B. D. and M. C. F. Proctor. 2000. Ecological gradients, subdivisions and terminology of north-west European mires. Journal of Ecology 88:187-203.

Worley, I. 1980. Ancient environments and age of non-glaciated terrain in southeastern Alaska. National Geographic Society Research Reports (1971).

CHAPTER 1

Calcareous fen vegetation and ecology, Chichagof Island, southeastern Alaska, USA

ABSTRACT

I described the vegetation, environment and ecological gradients within two calcareous fens in the Game Creek watershed, southeastern Alaska. My objectives were to complete a detailed floristic analysis and to quantify the hydrological and geochemical conditions related to species composition. Three community types were characterized within each site using multivariate analyses. Seventy-four vascular taxa were identified in the 140-m^2 area sampled. Water table, soil pH, and soil nutrient variables were correlated with vegetation gradients. Mean soil and water pH was 6.6, mean electrical conductivity was 351 µS/cm, mean pore water calcium was 42 $mg \cdot L^{-1}$, and mean soil calcium was 3744 $g \cdot m^{-3}$. The presence of rare and peripheral plant taxa combined with unusual site geochemistry creates unique plant communities within the region.

1.1 INTRODUCTION

Calcareous fens are considered to be one of the rarest wetland types in North America (Leete 1994), and throughout the world these fens are associated with rare plant species as well as high biodiversity (Almendinger and Leete 1998b, MDNR 1993, Boyer and Wheeler 1989). Calcareous fens are defined as a wetland type with calcium-rich groundwater inputs, hydric soils, calciphilic vegetation, and circumneutral to alkaline pH (Almendinger and Leete 1998a). This extremely rich wetland type is found within the hydrologic discharge zone at the base of limestone outcroppings and ridges, or where wetland groundwater sources are in contact with carbonate lithology. The resulting hydrogeochemistry is distinct from the predominant bog and fen communities of the surrounding area, and as a result often houses unique plant communities.

Within southeastern Alaska, the unique plant communities present in calcareous fens are recognized for their high species diversity, as well as inclusion of ecologically marginal or disjunct species (McClellan et al. 2003). Wetlands are common throughout the coastal western hemlock biogeoclimatic zone of coastal British Columbia and southeastern Alaska. The predominant wetland type is the acidic bog, with poor to rich fens present in lesser amounts. The extremely rich calcareous fens are an uncommon type, and within southeastern Alaska they are rare due to the scattered and limited presence of carbonate rock combined with the glacial history of the region.

Only a few calcareous fens have been described within Alaska and British Columbia (MacKenzie and Moran 2004, McClellan et al. 2003, Racine and Walters 1994). Calcareous fens have been described in other regions of North America as well, including Colorado (Johnson and Steingraeber 2003), the Midwest (Almendinger and Leete 1998a, Bowles et al. 2005, Glaser 1990, Komor 1994, Reed 1985), New England (Motzkin 1994, Picking and Veneman 2004, Van Hoewyk et al. 2000), and Alberta, Canada (Slack et al. 1980, Vitt and Chee 1990). Bedford and

Godwin (2003) provided an excellent summary of published calcareous fen studies throughout the United States. A gross survey was completed within the Alexander Archipelago (southeastern Alaska) to determine whether or not calcareous fens, as defined by Minnesota Department of Natural Resources (MDNR), were present (McClellan et al. 2003). The authors concluded that some of the criteria used by MDNR were met in two of the five sites sampled, but that regional differences may require criteria specific for the temperate rainforest of southeastern Alaska. This study is the first to undertake a more detailed investigation of the ecological characteristics of two calcareous fens within southeastern Alaska and the larger coastal western hemlock biogeoclimatic zone. For this project, one of the research sites was selected from the two calcareous fens identified by McClellan et al. (2003), while the second site was selected due to the presence of a disjunct dwarf birch population (*Betula glandulosa* Michx.).

The purposes of this study were to complete a detailed floristic analysis and quantify the hydrological and geochemical conditions related to species composition within two calcareous fens in the region. Specifically, I 1) described the vegetation communities within each of the two calcareous fens, 2) described the environmental conditions with comparisons between sites and between community types within each site and 3) explored the relationship between the environmental variables and the vegetation patterns within each of the two fens. This intensive within-site sampling aimed to characterize the vegetation and ecology of each site.

1.2 METHODS

1.2.1 Geologic and hydrogeomorphic setting

The two research sites selected for study are along a Game Creek tributary (57°58'12" N, 135°26'22"W), located on Chichagof Island, a northern outer island of the Alexander Archipelago in southeastern Alaska (Figure 1.1). The Game Creek watershed is roughly 18-km

long and 4-km wide at its widest point, representing the classic broad, glaciated U-shaped valley. The Kennel Creek Limestone formation is a prominent ridge roughly 1000 m in elevation on the northeast side of the Game Creek valley. The formation includes limestone with dolomite and limestone breccia, small amounts of shale and siltstone, and rare polymictic conglomerates (Karl 1996). The dominant rock type on the toeslope is calcareous graywacke with carbonate clasts, fossil fragments, subordinate feldspar, quartz, and volcanic rock fragments. The valley bottom is comprised of glaciomarine till, the product of extensive glacial activity in the region. Calcium rich water from this Kennel Creek marble formation discharges into the two research sites located in the transition zone between the toeslope and the valley bottom.

1.2.2 Climate

Climate is typical of a perhumid rainforest with mild winters and cool summers (Alaback 1996). Mean temperatures at sea level are 10°C in the summer and 0°C in the winter, and mean annual rainfall is 254 cm (Nowacki et al. 2001). Precipitation is heaviest September into November, and the driest months are March and April. The summer of 2004 was warm with record high temperatures in June, July and August (NOAA 2005); additionally, a mild April caused an early "leaf-out" with robust growth in vegetation by mid-May. In conjunction with above-average temperatures, precipitation records from Sitka were below normal during the growing season (May - September) (Table 1.1). Sitka is the closest station to the research site with consistent monthly data that likewise falls within the same precipitation isocline (Nowacki et al. 2001).

1.2.3 Vegetation

The predominant vegetation on the mountain slopes of Chichagof Island is Western hemlock (*Tsuga heterophylla* (Raf.) Sarg.) - Sitka spruce (*Picea sitchensis* (Bong.) Carr.) forest with Sitka alder (*Alnus viridis* (Chaix) DC. ssp. *sinuata* (Regel) A.& D. Löve) and salmonberry

(*Rubus spectabilis* Pursch) forming dense thickets in the avalanche chutes. Wetlands within the transition from toeslope to valley bottom are diverse floristically. Shrub-dominated and herbaceous-dominated fens are interspersed with forested wetlands. The forested wetlands transition to Western hemlock - Sitka spruce forests on the well-drained sites along waterways and on alluvial fans. The valley bottom is a mosaic of forested wetland and blanket bog, with open Sitka spruce stands in the riparian zone of Game Creek.

1.2.4 Site descriptions

Both research sites selected for study are shrub fens 2-km distant within the same watershed and fall within the discharge zone of the Kennel Creek limestone formation. These two sites differ primarily in the presence or absence of *Betula glandulosa* Michx., which is disjunct on Chichagof Island from the main mainland distribution on the northern and eastern side of the Coastal Mountain Range. The site with the disjunct birch population is hereafter referred to as the *B. glandulosa* site, and the non-birch site as the *Salix barclayi* Anderss. site. The sites are roughly 100 m above sea level, located at the base of a massive limestone ridge. Mean slope for both sites is 3% with a southwest aspect. The terracing present in both sites is likely the result of down-cutting over time from the tributary that runs along the base of the slope.

The terracing in both sites corresponded with apparent differences in vegetation. Terrace 1 in the *B. glandulosa* site is the highest in elevation, followed along a topographic gradient by terraces 2, 3, and 4 (Figure 1.2). The vegetation of terrace 1 is a mixture of graminoids and forbs, forming a 20-m wide band between forest and shrub fen communities. Dense shrubbery covers terrace 2, with a stream crossing from the north edge of the fen into the center midway through terrace 2. The shrub fen vegetation is more open on terrace 3, with a greater component of graminoid and forb species in the understory. The dominant vegetation is graminoid-forb on

terrace 4, with scattered shrubs and the occasional conifer. The stream is not contained through this terrace, resulting in frequent flooding across a wide swath of the terrace.

The *S. Barclayi* site is located on a terraced alluvial fan (Figure 1.2). The stream at this site is ephemeral, with surface flow only during periods of heavy snowmelt in the spring. The rest of the year the flow is subterranean on the backslope before discharging into the wetland. The upper terraces of the *S. barclayi* site sit on a carbonate deposition from an apparent debris flow. The vegetation on terrace 1 is a mixture of open shrubs, graminoids and forbs. A low-lying area falls in the middle of the terrace, serving as a drainage through the site. Terrace 2 is smaller as a result of a forested wetland band that follows the drainage that began in terrace 1. The vegetation is dominated by shrubs, with graminoids and forb species present. The vegetation on terrace 3 is dominated by sedge-forb wet meadow species. Ponding occurs on terrace 4 before the wetland discharges into the Game Creek tributary and transitions to forested communities. Vegetation consists of graminoid fen and shallow aquatic species. This terrace is similar in size to terrace 2, constrained by the adjacent stream. Deer browse of *S. barclayi* maintains the average height of the shrub at approximately 0.5 m.

1.2.5 Vegetation sampling

I used a stratified random sample design in both sites (*B. glandulosa* N=19, *S. barclayi* N=16). Sample size varied by terrace proportional to the terrace size, with a minimum of three plots per terrace (n=3 to n=6). I subjectively stratified the sites by terrace based on visual variations in vegetation as well as elevation differences. Species composition and descriptions of the variation between terraces within each site and between sites were measured using 4-m^2 plots. I visually estimated vegetation cover using an adjusted Braun-Blanquet cover score for each vascular plant species in late July 2003, the peak of the growing season (<1% = cover class 1, 1-5% = cover class 2, 6-25% = cover class 3, 26-50% = cover class 4, 51-75% = cover class 5, 76-

100 % = cover class 6). All vascular taxa were identified to the species or intraspecific level with the exception of *Viola* due to the inability to identify to the species level in the absence of flowers. Vascular plant nomenclature follows Hultén (1968).

Water and soil sampling were associated with each vegetation plot so as to relate measured environmental variables measured to vegetation patterns.

1.2.6 Water sampling

I measured the water table in shallow groundwater wells placed at each plot center as well as by pressure transducers placed on each terrace. The wells were constructed from 2.54-cm inside diameter PVC pipe 50-cm long. The bottoms were capped and the lower 25 cm was perforated. Paired wells were placed at plot center at 25-cm and 50-cm depths, flushed, pumped and allowed to equilibrate before sampling occurred. The 50-cm wells were an addition in 2004 due to a lower than expected water table. The water table was measured every other month during the growing season using a manual electronic sensor (May, July and September). I installed pressure transducers (Global Water, Inc.) at 100-cm depth on all terraces to record the water table every half hour during the growing season. When the water was present I field-checked the pressure transducer records with shallow well measurements.

I extracted pore water samples and measured pH and electrical conductivity with a YSI-85 multi-parameter meter. Following these measurements, samples were kept on ice for four to six hours, filtered using a pre-ashed 0.45-μm glass-fiber filter, and frozen until analysis at the Forest Sciences Laboratory in Juneau, AK. High temperature digestion and combustion on the Shimadzu TOC-V were used to analyze total nitrogen, total carbon, and total inorganic carbon. The ascorbic acid/molybdate method (Murphy and Riley 1962) was used to determine soluble-reactive phosphorus (SRP). Total phosphorus was analyzed using the potassium persulfate digest in conjunction with ascorbic acid (EPA 1983). Cations were analyzed using the Dionex-1500 Ion

Chromatography System. Anions were measured using the Dionex-2500 Ion Chromatography System with a carbonate scrubber.

A loss of sample points occurred when bears excavated the shallow wells, as well as when the water table dropped below the depth of the wells. I reinstalled excavated wells for sampling on the subsequent visit, and without bimonthly sample collection at every plot I pooled samples across the growing season for each plot.

1.2.7 Soil sampling

In July 2004 I took soil samples 1.0 m from plot center at 25-cm depth for characterizing soil morphology and soil nutrients. I determined bulk density using the core method (Blake and Hartge 1986). The soil samples taken for chemical analysis were kept on ice for four to six hours and then frozen until analysis at the Palmer Soils Laboratory in Palmer, AK. Chemical analyses were run on samples air-dried and passed through a 2-mm sieve. Percent organic matter was determined by ashing samples at 400° C (Soil Survey Staff 1996). Percent carbon and percent nitrogen were measured by the dry combustion method with the LECO CHN 1000. Percent phosphorus was analyzed via the perchloric acid digestion method (Soil Survey Staff 1996) and analyzed on the Optima XL ICP 3000. Exchangeable nutrients were quantified using the Mehlich-3 method (Mehlich 1984) with extracts analyzed on the Optima XL ICP 3000. Due to the variability in soil morphology, I converted all chemical quantifications from a weight to a volume basis for analysis.

1.2.8 Data Analysis

I used PC-Ord Version 4.1 (McCune and Mefford 1999) to perform cluster analysis and ordination of the vegetation data. Rare species, defined as those present in two or fewer plots, were removed from the dataset so that the resulting distance matrices would fit within acceptable limits of normality (McCune 1997). No relativization of species data occurred because

abundance was of interest in addition to presence/absence data. The resulting *B. glandulosa* matrix had 19 plots and 40 species; the *S. barclayi* matrix had 16 plots and 21 species.

Plots were grouped into community types based on species presence and abundance using agglomerative cluster analysis (CLUSTR), a hierarchical method that begins with an individual plot and merges plots until all are in one group. I used the Ward method with Euclidean distance for its reliability in classifying groups without distortion, producing one dendrogram for each site. The ideal would have been to use the same distance measure for both the classification and the ordination; however, the use of cluster techniques in grouping makes the choice of distance measures less important if the distance measure is compatible with the clustering method used (McCune and Grace 2002). I used Indicator Species Analysis (ISA) (Dufrene and Legendre 1997) to select the most informative level for pruning the dendrogram. ISA computes an indicator value for each species from the relative abundance and relative frequency within a particular group. Indicator values range from 0 to 100 percent, with 100 percent as a perfect indication that the species has complete fidelity with a particular group. I then used the Monte Carlo method to test the significance of the highest indicator against the null hypothesis that the highest indicator value is no larger than would be expected by chance (McCune and Mefford 1999). The most meaningful cluster step for making group determinations was decided from the highest number of indicator species and the lowest average Monte Carlo p-value of all species at a particular cluster step. This process retained the greatest amount of information within the dendrogram while also minimizing the number of groups.

I selected the nonmetric multidimensional scaling (NMS) technique (Kruskal 1964, Mather 1976) to look for gradients represented by species patterns. This ordination tool was designed for vegetation data that may be non-linear, non-normally distributed or discontinuous, and that may have multiple gradients of interest (McCune and Grace 2002). NMS was selected

as the ordination tool as it produces robust results with respect to ecological data in an indirect gradient analysis. I used a random starting configuration under the manual function to determine the best dimensionality for each site separately. All possible solutions were analyzed, with an instability criterion of .000005, 500 iterations, 50 runs through each real dataset, and 50 runs with the randomized dataset. The randomized dataset provides the basis for the Monte Carlo test of NMS extracting stronger than expected axes. The Sorensen distance measure (city block) was used in all ordination analyses. I used Bray-Curtis (Beals 1984) coordinates obtained in a previous ordination as a seed for the final ordination. Using an ordination method other than NMS has been suggested to avoid the problem of the local minima producing ordinations with strong geometric patterns (McCune and Grace 2002). The robustness of the solution obtained was further assessed by running the data several times using random number seeds. Non-parametric correlation coefficients (Kendall's tau) were used to compare the relationship of species' abundance to the position of plots along each axis in the exploratory analysis for gradients represented by species presence (plot position the product of cluster of species). The correlation coefficient was generated by an overlay of species against the axis ordination scores in PC-Ord, and the response was evaluated for true linearity in the scatter plot. I analyzed both sites separately during ordination and cluster analyses, as assessing both calcareous fens together masked gradients.

All soil and water data were analyzed using SAS (SAS Institute, Inc., Version 9.1 2002) to determine significant differences between plant communities within each site and between plant communities within each site. Differences between sites were determined with the Mann-Whitney two-sample test. Differences in environmental variables between communities were analyzed using the nonparametric Kruskal-Wallis analysis of variance test. I plot 95% confidence intervals for each of the significantly different variables to help assess the ecological importance

of the observed differences among community types (Di Stefano 2004). A non-parametric statistical test was determined best due to the small and unequal sample sizes as well as avoiding assumptions of normality in the response variables.

1.3 RESULTS

1.3.1 Plant communities

Analysis of vegetation by plot produced three plant community types within each site, only partially replicating the *a priori* stratification by terrace within each site as not all plots were separated by terrace (Figure 1.3). Within the *B. glandulosa* site, terrace 1 is defined by the dominance of *Carex sitchensis*, *Rubus arcticus* ssp. *stellatus*, and the absence of *B. glandulosa* (Table 1.2). Terrace 1 is hereafter referred to as a sedge meadow. Terraces 2 and 3 were clustered together into one community type, and, as a byproduct, this grouping is the most heterogeneous. This community type is dominated by *B. glandulosa* (average 70% cover), *Calamagrostis canadensis*, *Swertia perennis* and *Viola* sp. This cluster is hereafter referred to as the closed birch fen. Plots 3.5 and 3.6 of terrace 3 are grouped with terrace 4. The dominant plant species within this grouping were *B. glandulosa* (average 20% cover), *Dodecatheon jeffreyi* and *Parnassia fimbriata*. Terrace 4 is hereafter referred to as the open birch fen. Terraces 1 and 2 clustered together in the *S. barclayi* site dendrogram; this vegetation type is defined by *S. barclayi*, *S. perennis* and *Lysichiton americanum*. Plot 1.3 differened most from the other plots within this cluster. Terrace 3 is the most heterogeneous of the sites, and it is defined by *Castilleja unalaschensis* and the absence of *S. barclayi*. Terrace 4 is the most homogeneous terrace defined by the presence of *Menyanthes trifoliata*, *Carex flava*, *Carex echinata* and *Eriophorum russoleum*. Terraces 1 and 2 will be further referred to as the willow fen, terrace 3 as the sedge-forb wet meadow and terrace 4 as the buckbean waterway. Many of these species were

generalists across most of the site, but the dominance and frequency of occurrence distinguishes one terrace from another.

1.3.2 Floristics

A total of 74 species was identified in the 140-m^2 area sampled (35 plots). The *B. glandulosa* site had higher average species richness and overall diversity measures. Within the *B. glandulosa* site the closed birch fen community had the highest species richness, whereas in the *S. barclayi* site the wet forb-sedge meadow had the highest species richness (Table 1.3). In the *B. glandulosa* site, species richness values ranged from 16 to 19 (closed birch fen) species per plot, averaging 17.8 across all plots. Species richness values ranged from 14 (buckbean waterway) to 17 (wet sedge-forb meadow) species per plot, with an average of 15.7 species across all plots in the *S. barclayi* site. The heterogeneity represented by Whittaker's beta diversity indicated that the both sites have moderate species turnover among plots, with the *B. glandulosa* site (β=2.3) more heterogeneous than the *S. barclayi* site (β=1.6).

The species present in both sites were predominantly infrequent and low in abundance, with almost one-quarter of all species in only one plot (Table 1.2). Several species were dominant in both sites, with mean cover greater than 10%. Twenty-two percent of the species occurred in only one plot within the *B. glandulosa* site, with 34 % occurring in over one-third of the plots. Twenty percent of the species occurred in only one community type. Twenty-eight percent of the species occurred within the three community types in this site. Of the 41 species identified within the *S. barclayi* site, 20% occurred in only one plot while 44% occurred in over one-third of the plots. Comparing presence of species by community type, 31% occurred in the three community types whereas 22% occurred in only one community type.

1.3.3 Ordination of sample units in species space

Three-dimensional solutions for the ordination of sample units in species space were obtained to analyze species patterns for gradients in each site. For the *B. glandulosa* site, axis 1 separated the open birch fen from the remaining plant communities, and axis 3 separated the sedge meadow from the other community types (Figure 1.4a). The three axes explained 86.8% of the variation with axes 1 and 3 the strongest. In the *S. barclayi* site, the buckbean waterway was separated from the other plant communities along the gradient represented by axis 1, with plot 1.3 responding similarly (Figure 1.4b). Axis 1 represented half of the 91.1% cumulative variation. Both axes 2 and 3 represented weaker gradients separating the willow fen from the wet sedge-forb meadow and the buckbean waterway.

Eleven species within the *B. glandulosa* site and 13 species in the *S. barclayi* site showed a strong correlation to the ordination map (Figures 1.4a-b). Table 1.4 gives Kendall's tau correlation coefficients for species ranked strongly along one or more of the axes. These coefficients explore the relationships of species presence to underlying gradients represented by the axes. Within the *B. glandulosa* site, *D. jeffreyi* and *P. fimbriata* defined the open birch fen cluster along axis 1, while the greater cover of *Viola* sp and *Aster subspicatum* in terrace 2 spread the closed birch fen plots (Figure 1.4a). Along axis 3, the abundance of *C. sitchensis* and *R. arcticus* ssp. *stellatus* and the absence of *B. glandulosa* isolated the sedge meadow, while the abundance of *B. glandulosa*, *S. perennis* and *L. americanum* defined the loose grouping of the closed birch fen. Axes 1 and 3 explained 35% and 31% respectively of the 86.8% cumulative variation represented by the ordination. Axis 2 represented a weak gradient from the sedge meadow down to open birch fen. In the *S. barclayi* site, *M. trifoliata*, *C. flava* and *Carex disperma* strongly separated the buckbean water way along Axis 1, with *C. sitchensis*, *Angelica genuflexa* and *Platanthera dilatata* common in the other two communities (Figure 1.4b). This

axis represented 48.2 % of the cumulative variation. Along axis 3, *S. barclayi*, *Aster modestus*, *L. americanum* and *Angelica genuflexa* separated the willow fen from the wet sedge meadow defined by *Caltha leptosepala* ssp. *howellii*, *C. unalaschensis* and the absence of *S. barclayi* (Figure 1.4b). The gradient weakly represented by axis 2 showed *D. pulchellum* and *S. perennis* with several of the willow fen plots.

1.3.4 Hydrogeochemistry

Differences in the water table between sites were significant, with a shallower water table in the *S. barclayi* site (Table ~~1.5~~ 1.6). Comparisons of community types within each site were likewise significant (*B. glandulosa* X^2=10.72, P=0.0047 and *S. barclayi* X^2=5.72, P=0.0498). Overall, the water table increased in height with a drop in elevation. Depth below the surface ranged from 40 cm in the sedge meadow to 20 cm in the open birch fen in the *B. glandulosa* site, and from 25 cm in the willow fen to 10 cm in the buckbean waterway in the *S. barclayi* site (Figure 1.5).

In the analysis of soil-water differences between-sites, total nitrogen was significantly higher in the *B. glandulosa* site (Table 1.5). Potassium was significantly higher in the *S. barclayi* site, as were conductivity and pH. Interestingly, mean calcium did not follow the same pattern. With the exception of the soil-water pH and potassium, the significant within-site differences observed followed the significant between-site differences (Figure 1.5). Significant differences in nitrate concentrations within the *S. barclayi* site were driven by the higher concentrations in the willow fen (169 µg/L) and the low concentrations in the sedge-forb wet meadow (37.0 µg/L). Calcium was the dominant base cation in all communities, ranging from 17 – 136 mg/L. Values were highest in the closed birch fen within the *B. glandulosa* site and in the willow fen within the *S. barclayi* site. Conductivity was highest in the willow fen than the sedge-forb wet meadow and buckbean waterway within the *S. barclayi* site.

1.3.5 Soil nutrients

Soil chemicals were highly variable within each site and between sites (Figure 1.5, Table 1.5). Comparing between sites, the N:P ratios were significantly lower in the *B. glandulosa* site, as were nitrate and pH ($p<0.05$). Aluminum concentrations were significantly higher in the *B. glandulosa* site. Calcium was the dominant cation in all samples, ranging from 1004 to 8040 g/m^3. Generalizing, the base cations were higher in the *S. barclayi* site, whereas organic matter content and metal cations measured were lower.

The C:N ratios, N:P ratios, nitrate and aluminum concentrations, pH, and bulk densities were significantly different among plant communities within at least one of the sites (Figure 1.5). The C:N ratio was higher in the open birch fen (35) compared with the other communities in the *B. glandulosa* site(average 15). N:P ratios were highest in the closed birch fen and lowest in the open birch fen within the *B. glandulosa* site. Soil nitrate concentrations were highest in the willow fen in comparison to the other communities within the *S. barclayi* site. Bulk density and pH were likewise higher in the willow fen within the *S. barclayi* site, corresponding with the higher base cation concentrations. Aluminum was highest within the closed birch fen and sedge meadow of the *B. glandulosa* site.

1.3.6 Environmental variables and vegetation patterns

The underlying environmental gradients were explored by studying the correlation of environmental variables with vegetation patterns in each site. This was done by placing a passive overlay of the environmental variables in species space within the ordination map. Within the *B. glandulosa* site, open birch fen plots were separated along axis 1 by a higher water table and C:N ratio (Figure 1.6a, Table 1.6). The remaining loose cluster of closed birch fen plots at the opposing end of axis 1 had higher concentrations of soil ammonium and aluminum as well as sulfate and minimum calcium constituents in the water. The higher water total phosphorus and

SRP were correlated with axis 3 that separated the sedge meadow. In the *S. barclayi* site, several environmental factors had a moderately strong relationship to the vegetation patterns (Figure 1.6b, Table 1.6). The water table was one of the stronger driving gradients (Kendall's tau=0.552) within the site. Axis 1 best represented this gradient, separating the buckbean waterway from the remaining plant communities. Higher water total phosphorus and SRP were also correlated with this plant community. Plots 1.3 and 3.4 were also present along this axis due to their location in low-lying areas within their respective terraces. Water total nitrogen was correlated with the willow fen and the wet sedge-forb meadow to a lesser extent along axis 1. Soil pH, bulk density, and water total nitrogen and nitrate concentrations were strongly correlated with the willow fen communities along axis 3. Soil calcium, soil magnesium, total organic carbon, water pH, and conductivity were also correlated with this community along axis 3. The wet sedge-forb meadow species assemblage was at the lower end of the aforementioned environmental variables along axis 3. No environmental factors measured were correlated with this plant community.

1.4 DISCUSSION

1.4.1 Comparison of the Game Creek calcareous fens with other systems

1.4.1.1 Fen Chemistry

The two Game Creek calcareous fens sampled are unusual within the coastal western hemlock biogeoclimatic zone. Within the 6.9 million hectares of the Tongass National Forest in the Alexander Archipelago of southeastern Alaska, wetlands comprise roughly 30% of the land base (USDA 1997). The predominant wetland type is the acidic bog, and the fens present in the region are poor to moderately species rich, pH ranging 4.5 – 6.0 (MacKenzie and Moran 2004). Comparatively, the calcareous fens sampled have a circumneutral pH and plant assemblages that are uncommon within the region.

The two Game Creek wetlands are correctly classified as calcareous fens. The average pH of 6.1-7.1, average water calcium values of 31-55 mg/L, and specific conductivity of 220-496 µS/cm for each plant community falls within the ranges reported for calcareous fens within North America: pH 6.4-8.1, 10-120 mg/L Ca, and 110-1057 µS/cm specific conductivity (Almendinger and Leete 1998a, Bowles et al. 2005, Glaser et al. 1990, Johnson and Steingraeber 2003, Motzkin 1994, Picking 2002, Slack et al. 1980). However, water magnesium values within the Game Creek fen are much lower than that reported for other calcareous fens (0.3-0.8 mg/L compared with 11-50 mg/L), whereas the potassium values are much higher (9-18 mg/L compared with 0.4-4.7 mg/L). Exchangeable soil calcium values range from low to exceedingly high (4500 mg/kg to 21000 mg/kg weight basis). The lows are comparable with the average for New England (Picking 2002), while the highs dwarf the highs documented in the calcareous mires of Colorado (Johnson and Steingraeber 2003).

The absence of marl or tufa (carbonate precipitate) in the soils at the Game Creek fens differs from most but not all of the calcareous fen systems described in the literature. This may be the result of high rates of precipitation diluting and/or flushing bicarbonate out of the system. Almendinger and Leete (1998a) described how rates of peat accumulation could decrease the frequency and duration of soil saturation necessary for carbonate precipitates, as well as other mechanisms. The lack of carbonate precipitate may be a combination of the above factors or related to some other variables. Measuring carbonate content within the soil horizons would allow determination of carbonate-rich and carbonate-depleted zones, as well as the concentrations of carbonate for further study of why tufa and marl are not present within the Game Creek sites.

1.4.1.2 Species richness and indicators

Species richness values of 16 to 19 vascular taxa per 4-m^2 plot in the Game Creek sites were comparable to the averages reported for calcareous fen studies elsewhere in North America.

Average vascular and non-vascular species richness values in upstate New York ranged from 6 to 19 taxa in 1-m^2 quadrats (Drexler and Bedford 2002), in the New York region 26 to 78 per 25-m^2 area (Bedford et al. 1999) and in Massachusetts 55 to 80 species per 15-m^2 plot (Picking and Veneman 2004). It is likely that the somewhat lower species richness values found in the study of Game Creek calcareous fens are a regional characteristic, as the perhumid rainforest is noted for its moderate diversity when compared with other ecosystems (Alaback 1996). Moreover, the nonvascular taxa are absent from the Game Creek site results presented.

Two Alaska rare species were present within the Game Creek sites, *Galium kamtschaticum* and *Botrychium virginianum* ssp. *europaeum*, as were several uncommon species. A disjunct population of *B. glandulosa* located in Game Creek is the only documented location of this species in the Alexander Archipelago, with the nearest documented occurrence of *B. glandulosa* in the Wrangell-St. Elias alpine zone 150-km distant (University of Alaska Museum 2005). The Coastal Mountain range and saltwater create a biogeographical barrier to species dispersal within the Alexander Archipelago. Northern southeastern Alaska is known to house boreal species on the southern limit of their range, and the Game Creek fens had several. *Pyrola asarifolia* var. *purpurea* is somewhat common on the mainland, but uncommon on the islands. *Polemonium acutiflorum* is uncommon but present in low abundance elsewhere in the northern islands. *B. virginianum* ssp. *europaeum*, *Cystopteris fragilis*, *G. kamtschaticum, Malaxis brachypoda*, and *Carex saxatilis* are additional boreal species present in the Game Creek fens that are also uncommon throughout the northern islands.

Using vascular plant species as indicators of calcareous fens can be problematic, as environmental tolerances vary by region and few of the plant species within the Game Creek calcareous fens are restricted to these sites. Four species identified as calciphiles were present in the Game Creek sites: *C. fragilis*, *C. flava*, *Dodecatheon pulchellum*, and *P. fimbriata* (Hulten,

1968, Klinka et al. 1989). *D. pulchellum* is more an indicator of weakly alkaline than calcium-rich conditions within southeastern Alaska, as this species is common in the coastal intertidal zone but rare in wetland systems. *P. fimbriata* is an indicator of minerotrophy, but it is not restricted to sites that have calcium-rich waters within southeastern Alaska. Many of the species present within the Game Creek sites, e.g., *C. sitchensis* and *L. americanum* have a broad ecological tolerance. *B. glandulosa* is a further example, as it ranges from acidic wet to tallus scree elsewhere within its range.

Regional floristic differences compound difficulties in determining indicator species for calcareous fens as there is little overlap in the species shared. Where there is overlap, species that are indicators of calcareous fens elsewhere, such as *Carex livida*, (Slack et al. 1980), *Equisetum fluviatile* (Picking and Veneman 2004), and *Utricularia intermedia* (Glaser et al. 1990) are found in poor to moderately rich fens (pH 5.0 – 6.0) within southeastern Alaska. The alpine *Thalictrum alpinum* is the one species identified as an indicator (Johnson and Steingraeber 2003) that was present within the complex of Game Creek calcareous fens but not at one of the research sites. Broad studies of calcareous fens within the region would provide a list of indicator species, as well as unique species assemblages that indicate calcium-rich conditions. Such a study would document species and species assemblages present on the northern and southern limit of their range within southeastern Alaska.

1.4.2 Species patterns and ecological gradients

The water table was the strongest underlying gradient that corresponded to species patterns within both fen systems, as species composition changed along a dry to wet gradient (Figure 1.4a-b). Within the *B. glandulosa* site, *D. jeffreyi*, and *P. fimbriata* were associated with the higher water table, while *A. subspicatum* and *Viola* species were at the drier end of the water table gradient. The restriction of *M. trifoliata*, *C. flava*, and *C. echinata* to the higher water table

reflects a strong gradient within the *S. barclayi* site. Hydrology controls all facets of species composition, as it affects the suite of the fens' physical and chemical characteristics including anoxic conditions, peat accumulation, nutrient availability, redox potential, and other factors (e.g., Lambers et al. 1998, Mitsch and Gosselink 2000). The measured water table may have been lower than the normal, perhaps due to higher than usual evapotranspiration rates and robust vegetation growth during the exceptionally warm 2004 growing season. Unlike the other plant communities, the water table in the buckbean waterway was relatively static and at or near the surface through the growing season (Figure 1.5). The lower the water table, the greater the frequency and intensity of fluctuations observed throughout the growing season.

The groundwater discharging into the system is important in maintaining these plant communities, yet the absence of underlying gradients suggests that the high temporal and spatial variation of water chemistry may not be as strong of a factor influencing species composition as the soil. Alternatively, this absence may be an artifact of water sampling challenges presented by the variability of the spatial flow of water as well as the sensitivity of water to precipitation and evaporation. More frequent sampling over a period of years would be needed to quantify the range of variability and identify underlying gradients (e.g., Picking 2002).

The soil pH gradient underlying species' patterns within the *S. barclayi* site is likely caused by the depositional layer of carbonate near the surface. *S. barclayi* and *A. modestus* are the only species within the willow fen that respond to this gradient. The presence of this carbonate deposition does not create the abrupt changes in plant communities described elsewhere (e.g., Bowles et al. 2005, Carpenter 1995), nor are calciphiles concentrated within this plant community. No pH gradient was indicated by the vascular species present within the *B. glandulosa* site.

Both sites receive groundwater discharging from the same geological source, but geomorphological development has created different sets of conditions within each site. The active stream channel within the *B. glandulosa* site continues to alter conditions, as the stream had changed course within the open birch fen between site visits in 2003 and 2004. The stream migration has occurred over time through the closed and open birch fen communities, contributing to the variability in environmental parameters. The *S. barclayi* site does not have this active natural disturbance; however, the carbonate layer indicates that a large event deposited this alluvial material relatively recently.

1.5 CONCLUSIONS

My study was the first to describe calcareous fens in detail within the coastal western hemlock biogeoclimatic zone. This work contributes to our picture of rare plant communities and will improve both our understanding of the distribution of rare and uncommon plant populations and our ability to preserve these unique wetland systems. Additional work is needed to identify other calcareous fen community types across the Alexander Archipelago to capture the diversity of these rare plant communities. I show that in this perhumid region, species patterns within calcareous fens are most strongly influenced by water table and less so by soil and water chemistry. Further work would be required to tease out the influence of water chemistry upon plant composition. Such work might allow us to better manage the landscapes that these communities lie within to avoid disrupting the unique settings that produce calcareous fens in southeastern Alaska.

REFERENCES

Alaback, P. B. 1996. Biodiversity patterns in relation to climate: the Coastal Temperate Rainforests of North America. In *High-latitude Rainforests and Associated Ecosystems of the West Coast of the Americas*. R.G. Lawford, P.B. Alaback and E. Fuentes eds. Springer-Verlag, Inc., New York, NY, USA.

Almendinger, J. E. and J. H. Leete. 1998a. Peat characteristics and groundwater geochemistry of calcareous fens in the Minnesota River Basin, U.S.A. Biogeochemistry 43:17-41.

Almendinger, J. E. and J. H. Leete. 1998b. Regional and local hydrogeology of calcareous fens in the Minnesota River Basin, USA. Wetlands 18:184-202.

Amon, J. P., C. A. Thompson, Q.J. Carpenter and J. Miner. 2002. Temperate zone fens of the glaciated Midwestern USA. Wetlands 22:301-317.

Beals, E.W. 1984. Bray-Curtis ordination: an effective strategy for analysis of multivariate ecological data. Advances in Ecological Research 14:1-55.

Bedford, B. L. and K. S. Godwin. 2003. Fens of the United States: Distribution, characteristics, and scientific connection versus legal isolation. Wetlands 23:608-629.

Bedford, B. L., M. R. Walbridge and A. Aldous. 1999. Patterns in nutrient availability and plant diversity of temperate North American wetlands. Ecology 80:2151-2169.

Blake, G. R. and K. H. Hartge. 1986. Bulk density. In A. Klute (ed.) Methods of soil analysis. Part 1. Physical and mineralogical methods. 2nd. Ed. Agronomy 9:363-382.

Bowles, M. L., P. D. Kelsey and J. L. McBride. 2005. Relationships among environmental factors, vegetation zones, and species richness in a North American calcareous prairie fen. Wetlands 25:685-696.

Boyer, M. L. H. and W. D. Wheeler. 1989. Vegetation patterns in spring-fed calcareous fens: Calcite precipitation and constraints on fertility. Journal of Ecology 77:597-609.

Carpenter, Q. J. 1990. Hydrology and vegetation on a calcareous peat mound fen in southeastern Wisconsin. M.Sc. thesis, University of Wisconsin-Madison, Madison, WI, USA.

Chapin, F. S. III, P. A. Matson and H. A. Mooney. 2002. Principles of terrestrial ecosystem ecology. Springer-Verlag, New York, NY, USA.

Di Stefano, J. 2004. A confidence interval approach to data analysis. Forest Ecology and Management 187:173-183.

Drexler, J. Z. and B. L. Bedford. 2002. Pathways of nutrient loading and impacts on plant diversity in a New York peatland Wetlands 22:263-281.

Dufrene, M. and P. Legendre. 1997. Species assemblages and indicator species: the need for a flexible asymmetrical approach. Ecological Monographs 67:345-366.

Environmental Protection Agency (EPA). 1983. Phosphorus, All Forms. Method 365.1 (Colorimetric, Automated, Ascorbic Acid). pp.365-1.1 -- 365-1.7. In Methods for Chemical Analysis of Water and Wastes, EPA-600/ 4-79-020. U.S.E.P.A., Cincinnati, OH, USA.

Glaser, P. H., Janssens, J. A. and D. I. Siegel. 1990. The response of vegetation to chemical and hydrological gradients in the Lost River Peatland, northern Minnesota. Journal of Ecology 78:1021-1048.

Hultén, E. 1968. *Flora of Alaska and Neighboring Territories*. Stanford University Press, Stanford, CA, USA

Johnson, J. B. and D. A. Steingraeber. 2003. The vegetation and ecological gradients of calcareous mires in the South Park valley, Colorado. Canadian Journal of Botany 81:201-219.

Karl, S. 1996. Preliminary geologic map of northeastern Chichagof Island, Alaska. Open File report 96-53. U.S. Geological Service, Denver, CO, USA.

Klinka, K., V. J. Krajina, A. Ceska and A. M. Scagel. 1989. *Indicator plants of Coastal British Columbia*. University of British Columbia Press, Vancouver, BC, Canada.

Komor, S. C. 1994. Geochemistry and hydrology of a calcareous fen within the Savage Fen wetlands complex, Minnesota, USA. Geochimica et Cosmochimica Acta 58:3353-3367.

Kruskal, J. B. 1964. Nonmetric multidimensional scaling: a numerical method. Psychometrika 29:115-129.

Lambers, H., F. S. Chapin III and T. L. Pons. 1998. Plant Physiological Ecology. Springer, New York NY, USA.

Leete, J. H. 1994. Minnesota defends fens. Water, Environment, and Technology 6:24-25.

MacKenzie, W. H. and J. R. Moran. 2004. Wetlands of British Columbia: a guide to identification. Land Management Handbook No. 52. Research Branch, British Columbia Ministry of Forestry, Victoria, B.C., Canada.

Mather, P. M. 1976. Computational methods of multivariate analysis in physical geography. J. Wiley and Sons, London, UK.

McClellan, M. H., T. Brock and J. F. Baichtal. 2003. Calcareous fens in southeast Alaska. PNW-RN-536. USDA Forest Service, Pacific Northwest Research Station, Juneau, AK, USA.

McCune, B. 1997. Influence of noisy environmental data on Canonical Correspondence Analysis. Ecology 78:2617-2623.

McCune, B. and J.B. Grace. 2002. Analysis of Ecological Communities. MjM Software Design, Gleneden Beach, OR, USA.

McCune, B., and M. J. Mefford. 1999. PC-ORD Multivariate analysis of ecological data. Ver. 4. MjM Software, Gleneden Beach, OR, USA.

Mehlich, A. 1984. Mehlich 3 soil test extractant: A modification of Mehlich 2 extractant. Communications in Soil Science and Plant Ananlysis 15:1409-1416.

Minnesota Department of Natural Resources (MDNR). 1995. Technical criteria for identifying and delineating calcareous fens in Minnesota. Minnesota Department of Natural Resources, St. Paul, MN, USA.

Mitsch, W. J. and J. G. Gosselink. Wetlands. 3rd ed. John Wiley & Sons, Inc., New York, NY, USA.

Motzin, G. 1994. Calcareous fens of western New England and adjacent New York State. Rhodora 96:44-68.

Murphy, J. and J. P. Riley. 1962. A modified single solution method for the determination of phosphate in natural waters. Analytica Chimica Acta 27:26-30.

National Oceanic and Atmospheric Association. 2005. http://www4.ncdc.noaa.gov/cgi-win. (accessed 12/2005).

Nowacki, G., M. Shephard, P. Krosse, W. Pawuk, G. Fisher, J. Baichtal, D. Brew and E. Kissinger. 2001. Ecological Subsections of Southeast Alaska and Neighboring Areas of Canada. R10-TP-75. USDA Forest Service, Alaska Region, Anchorage, AK, USA.

Picking, D. J. 2002. Vegetation patterns and associated hydrogeochemical cycles in a calcareous sloping fen of southwestern Massachusetts. Ph.D. Dissertation. University of Massachusetts, Amherst, MA, USA.

Picking, D. J. and P. L. M. Veneman. 2004. Vegetation patterns in a calcareous sloping fen of southwestern Massachusetts, USA. Wetlands 24:514-528.

Racine, C. H. and J. C. Walters. 1994. Groundwater-discharge fens in the Tanana Lowlands, Interior Alaska, U.S.A. Arctic and Alpine Research 26:418-426.

Reed, D. M. 1985. Composition and distribution of calcareous fens in relation to environmental conditions in southeastern Wisconsin. MS. Thesis, University of Wisconsin-Milwaukee, WI, USA.

SAS Institute, Inc. 2002. SAS Version 9.1. SAS Institute, Inc. Cary, NC, USA.

Slack, N. G., D. G. Vitt and D. G. Horton. 1980. Vegetation gradients of minerotrophically rich fens in western Alberta. Canadian Journal of Botany 58:330-350.

Soil Survey Staff. 1996. Soil survey laboratory methods manual. Version No.4.0. USDA NRCS. Soil Survey Investigations Report No. 42. U.S. Govt. Print. Office, Washington, DC, USA

University of Alaska Museum. 2005. Arctos Database. http://www.uaf.edu/museum/herb/index.html. Fairbanks, Alaska. (accessed 12/15/2005).

USDA. 1997. Tongass National Forest Land and Resource Management Plan. R10-MB-338dd. USDA Forest Service Region 10, Juneau, AK, USA.

Van Hoewyk, D., P. M. Groffman, E. Kivita, G. Mihocko and G. Stevens. 2000. Soil nitrogen dynamics in organic and mineral soil calcareous wetlands in eastern New York. Soil Sciences of America Journal 65:2168-2173.

Vitt, D. H. and W. H. Chee. 1990. The relationships of vegetation to surface water chemistry and peat chemistry in fens of Alberta, Canada. Vegetatio 89:87-106.

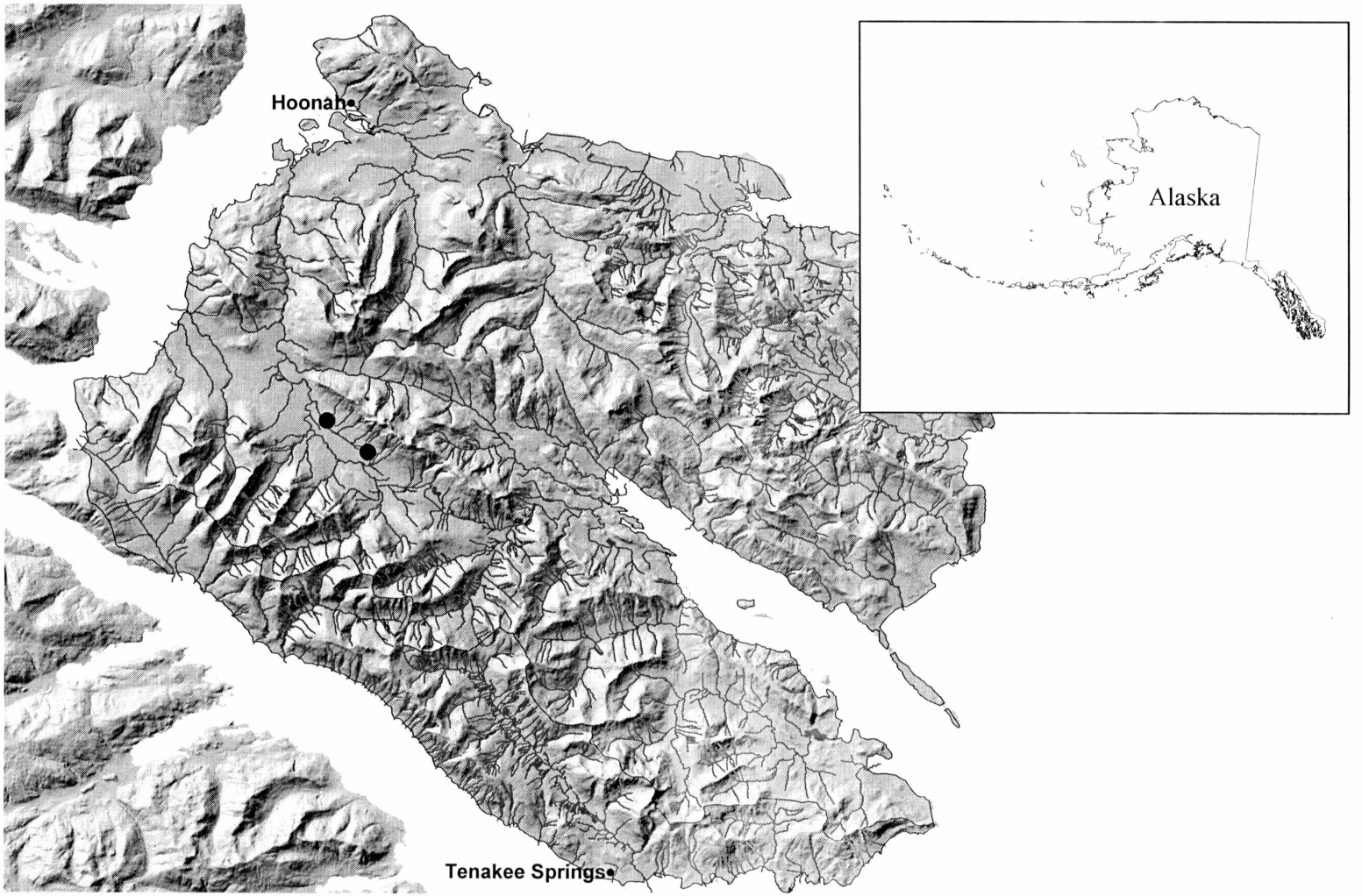

Figure 1.1 Research area in Game Creek, Chichagof Island.

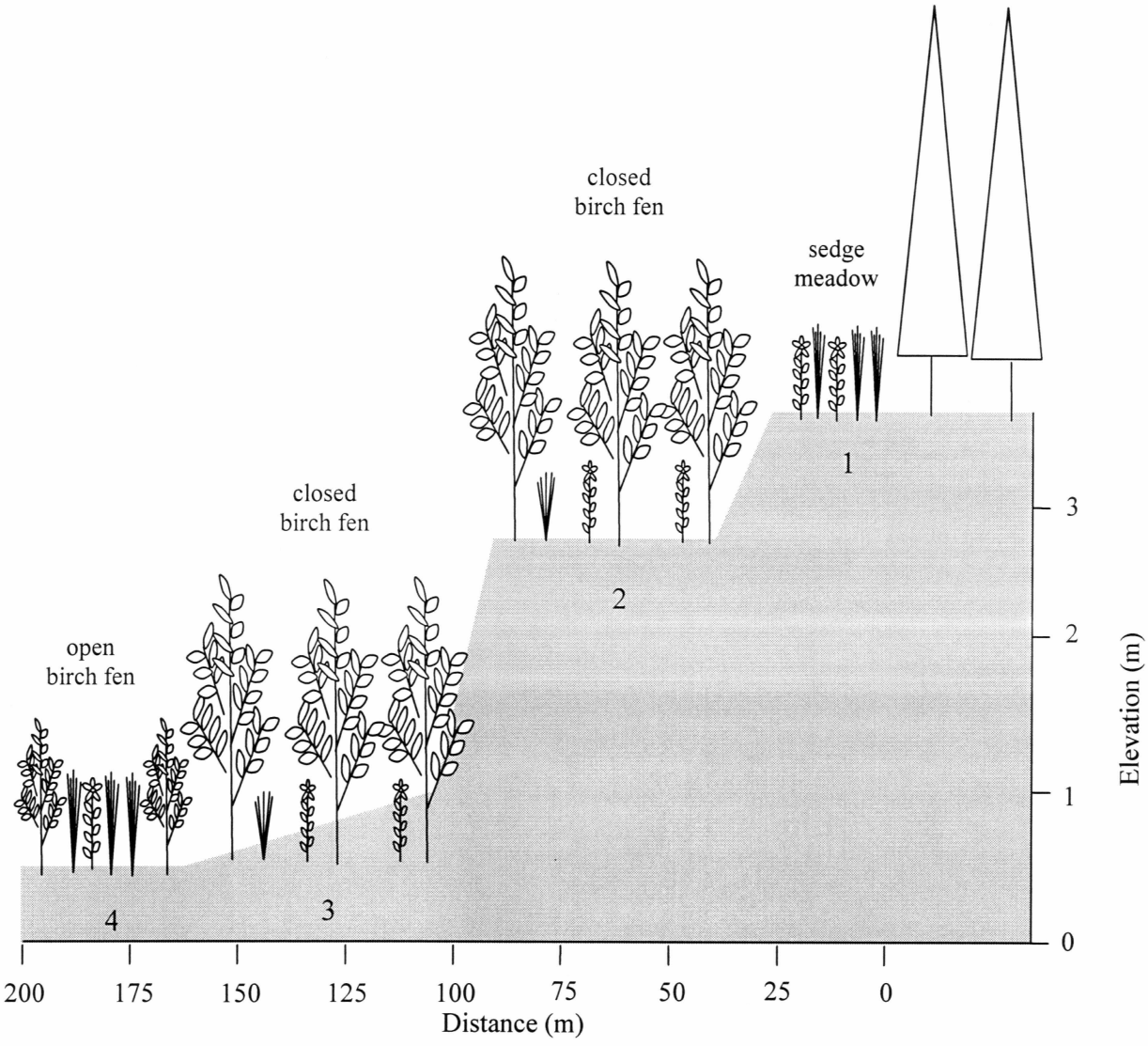

Figure 1.2 Schematic of both sites, Game Creek, Alaska. Schematic of *B. glandulosa* (top) and *S. barclayi* (bottom) sites showing the number, size, gradient and general vegetation of the terraces.

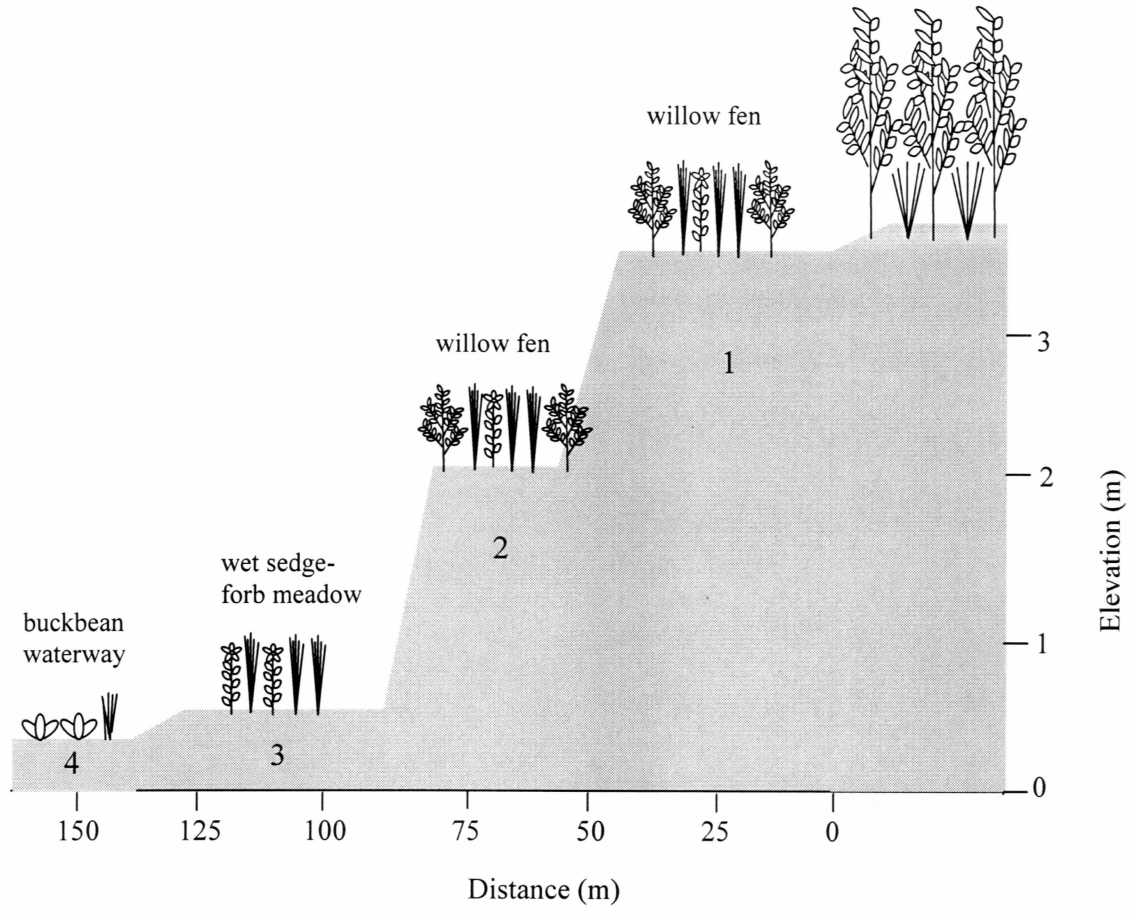

Figure 1.2 Continued. Schematic of both sites, Game Creek, Alaska.

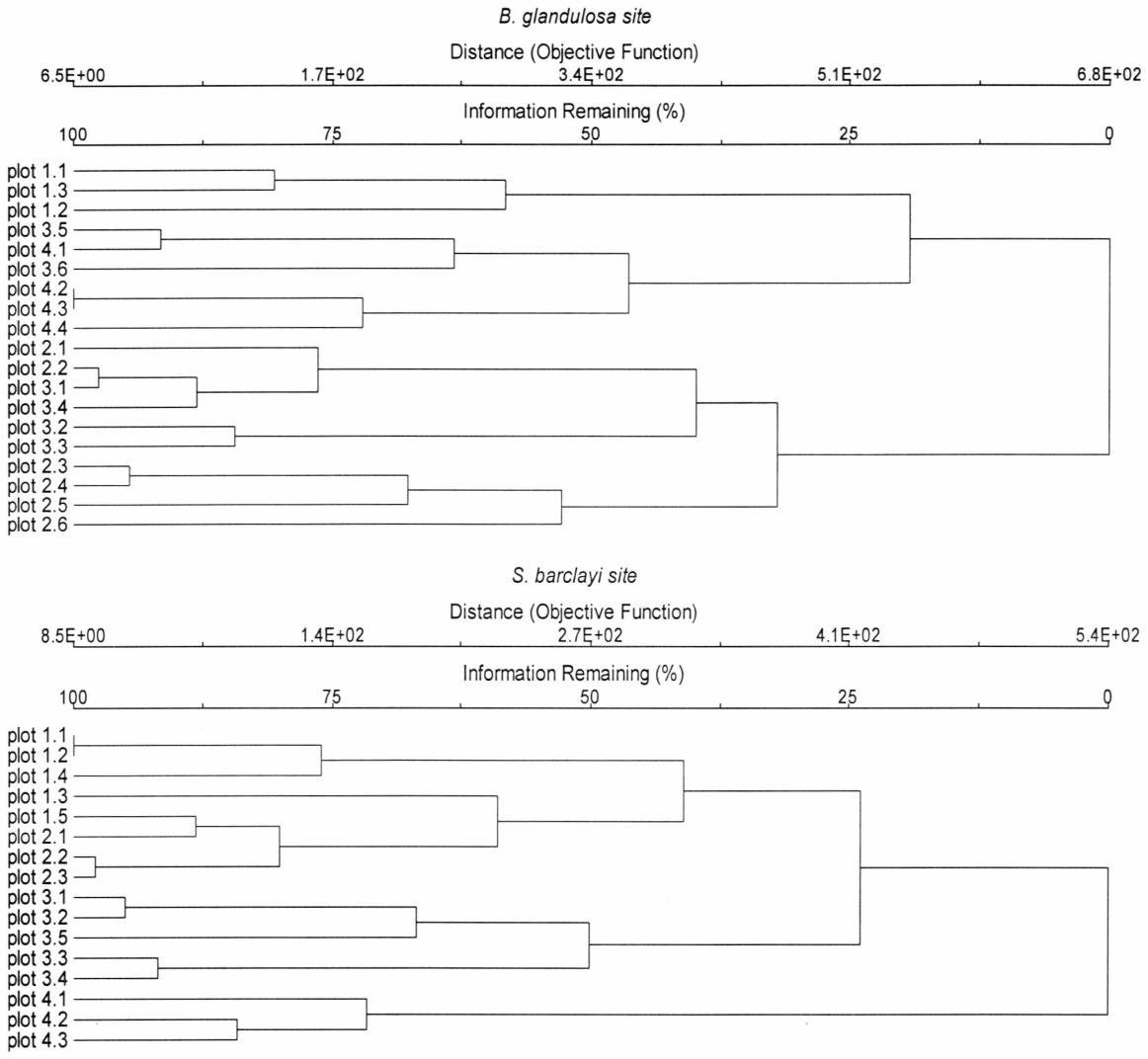

Figure 1.3 Agglomerative cluster dendrograms. Agglomerative cluster dendrogram for the *B. glandulosa* (top) and *S. barclayi* (bottom) sites produced from vegetation cover and abundance. The first digit refers to the terrace position, the second to the replicate plots within each terrace.

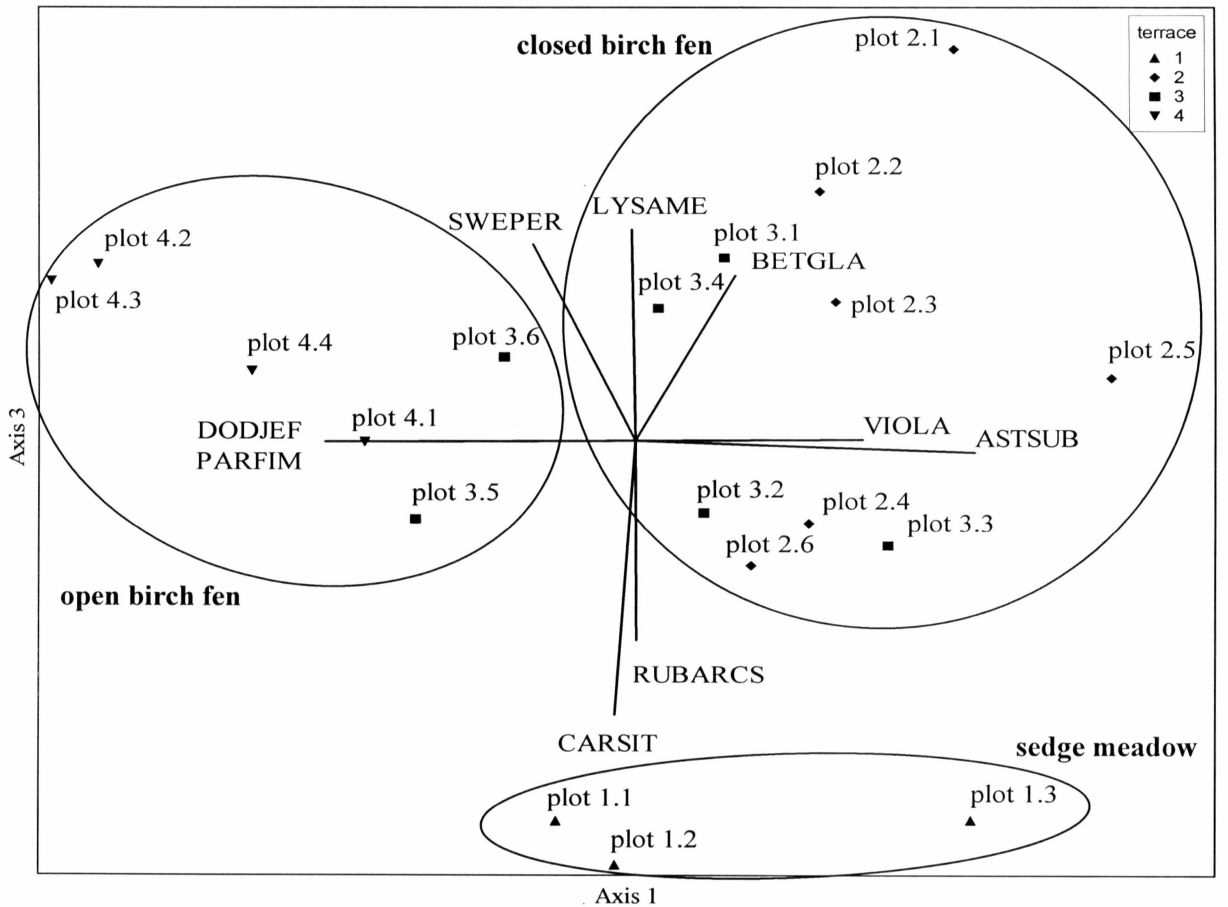

Figure 1.4 Joint plot with correlation of species in species space. Figures 1.4a-b: Joint plot showing correlation of indicator species with the base plot NMS ordination of species in species space. The length of the vectors indicates the strength of the species' relationship with the axis. a) In the *B. glandulosa* site the proportion of variation represented by each axis was the following: Axis 1, $R^2 = 0.349$; Axis 2, $R^2 = 0.206$ and Axis 3, $R^2 = 0.313$. Cumulative variation = 86.8%. b) The proportion of variance represented by each axis space in the *S. barclayi* site was the following: Axis 1, $R^2 = 0.482$; Axis 2, $R^2 = 0.187$ and Axis 3, $R^2 = 0.242$. Cumulative variation = 91.1%.

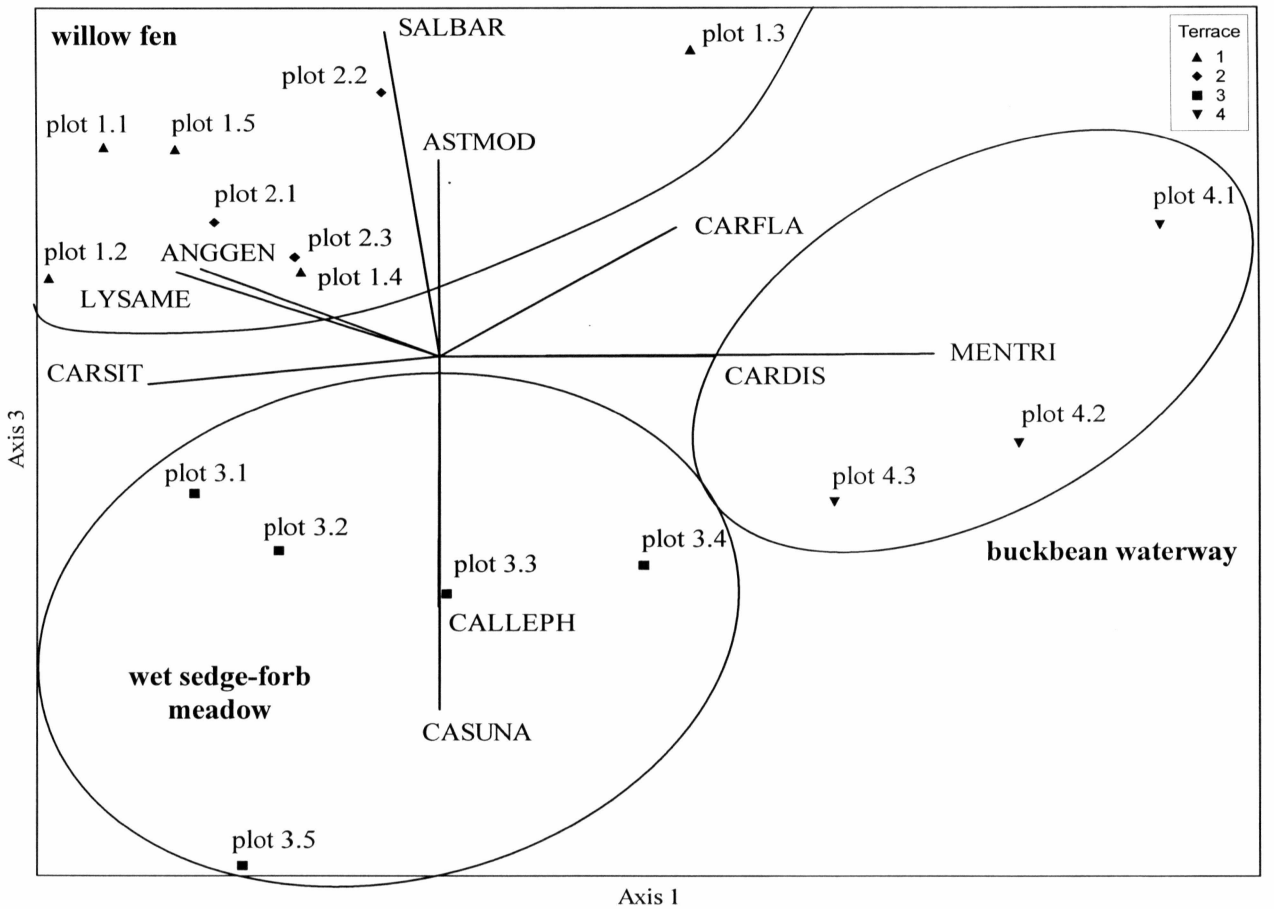

Figure 1.4 Continued. Joint plot with correlation of species in species space.

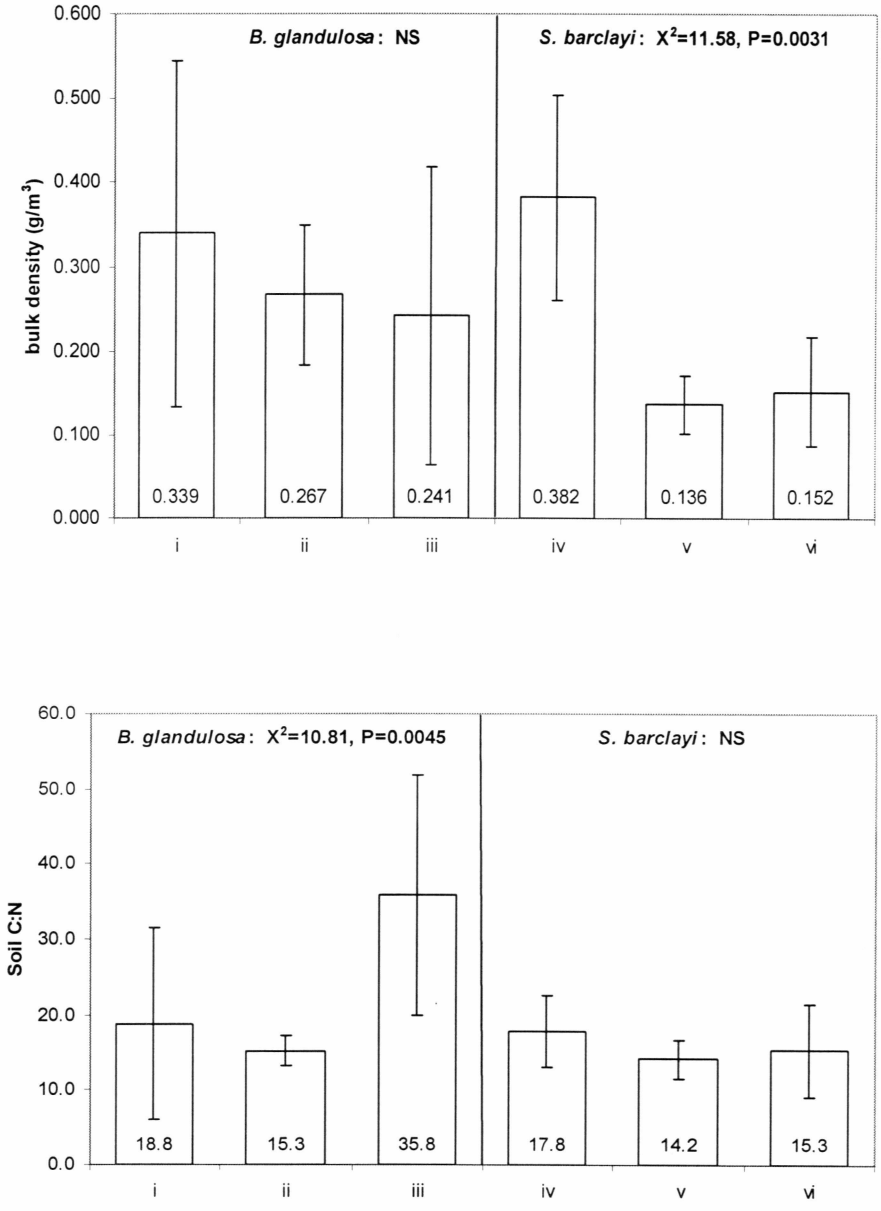

Figure 1.5 Comparison of environmental variables by community type by site. Distribution of select significant environmental variables from the six community types with Kruskal-Wallis test statistics, community type mean and 95% confidence interval error bars. *B. glandulosa* community types: i = sedge meadow (n=3), ii = closed birch fen (n=10), iii = open birch fen (n=6); *S. barclayi* community types: iv = willow fen (n=8), v = wet sedge-forb meadow (n=5), vi = buckbean waterway (n=3).

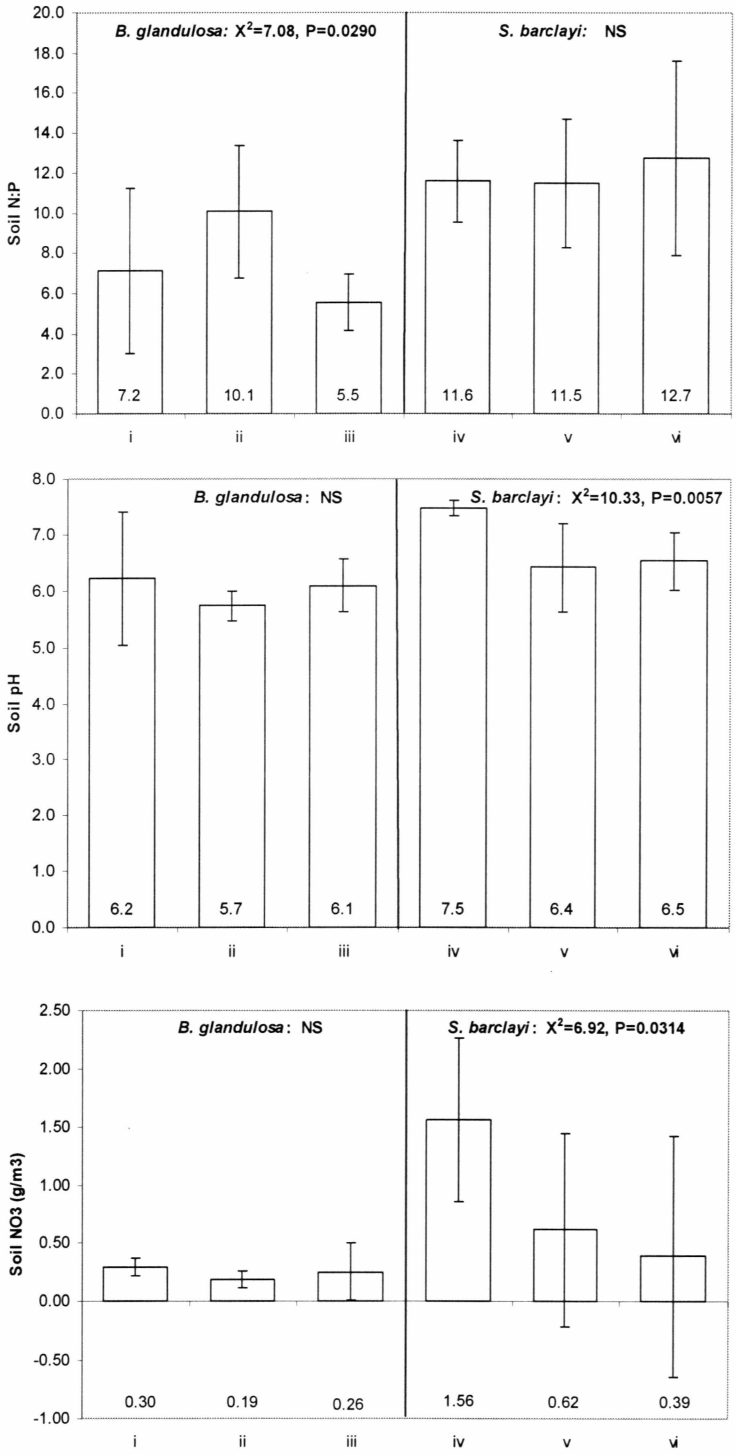

Figure 1.7 Continued. Comparison of environmental variables by community type by site.

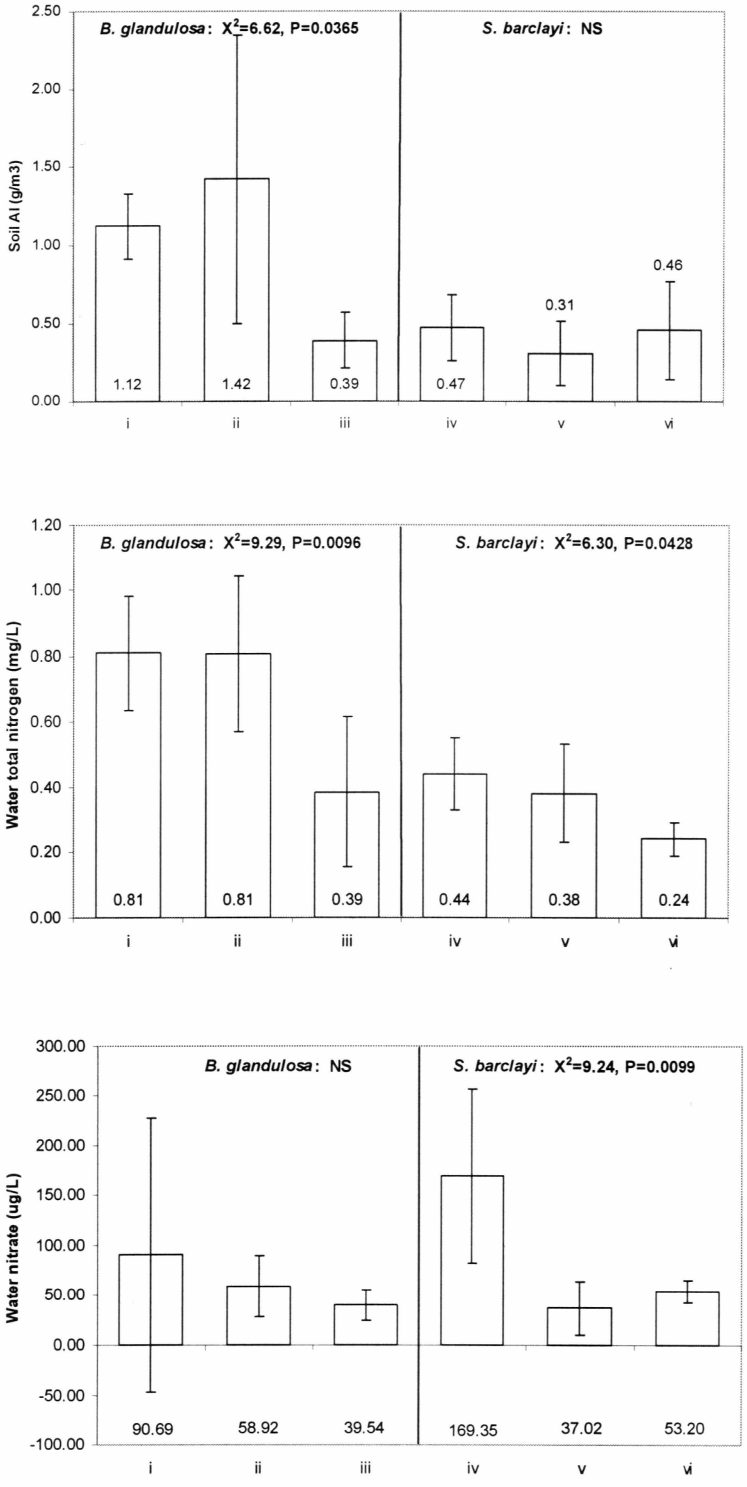

Figure 1.5 Continued. Comparison of environmental variables by community type by site.

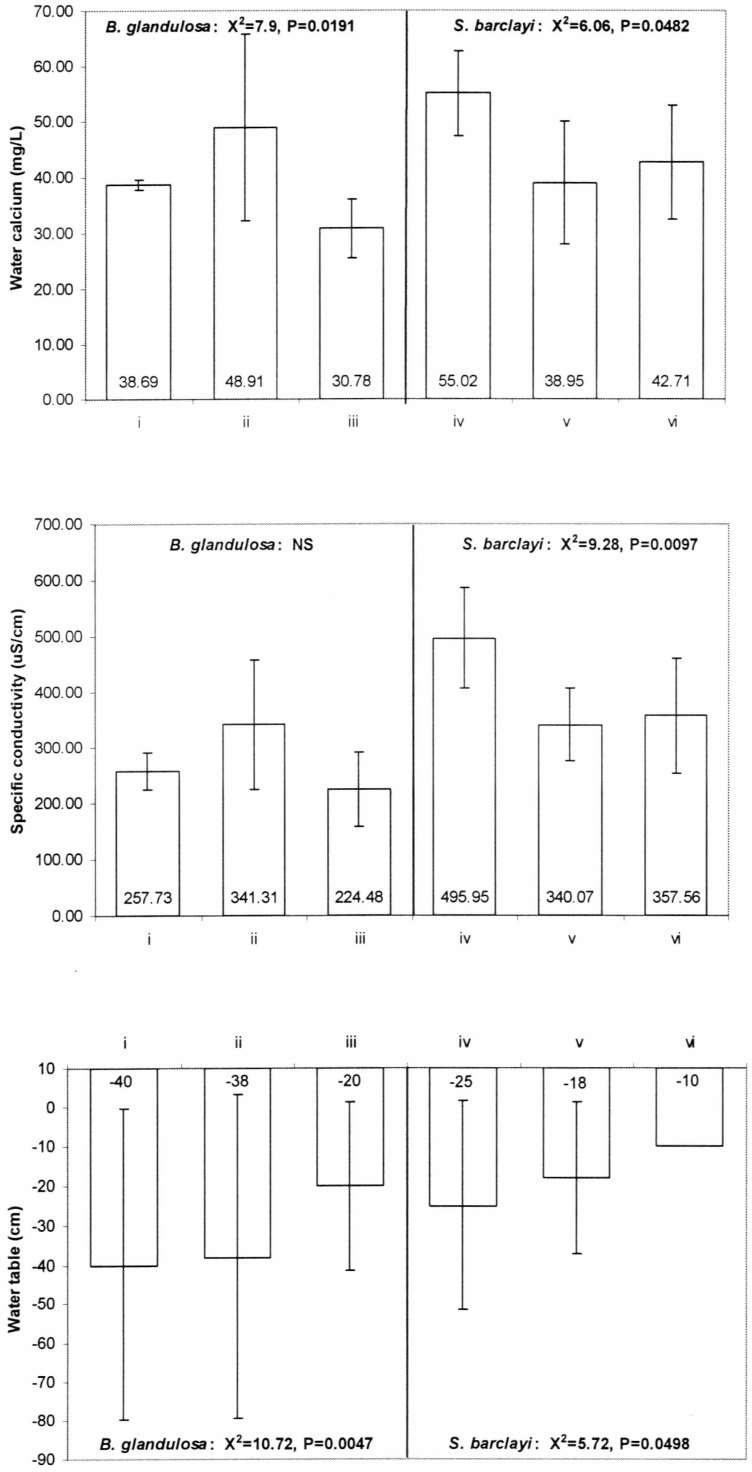

Figure 1.5 Continued. Comparison of environmental variables by community type by site.

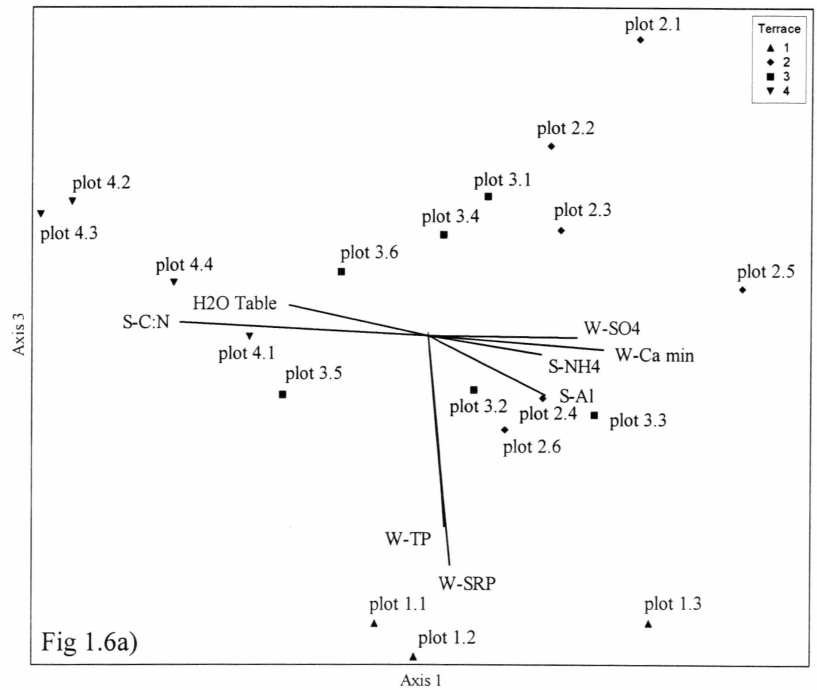

Fig 1.6a)

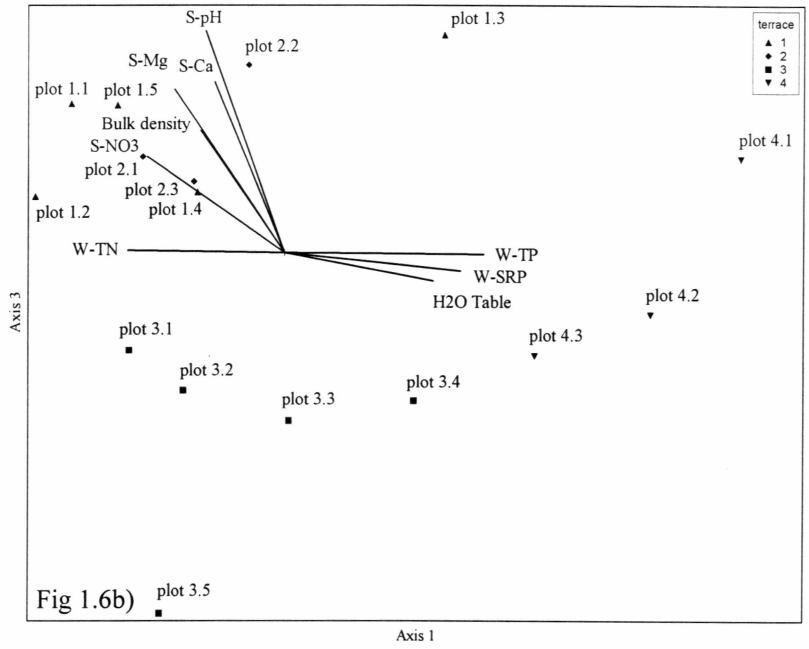

Fig 1.6b)

Figure 1.6 Joint plot overlay of environmental variables in species space. Figures 1.6a-b: Joint plot showing correlation of environmental variables with the base plot NMS ordination of species in species space. The length of the vectors indicates the strength of the variables' relationship with the axis. a) The proportion of variance represented by each axis in the *B. glandulosa* site was the following: Axis 1, $R^2 = 0.349$; Axis 2, $R^2 = 0.206$ and Axis 3, $R^2 = 0.313$. Cumulative variation = 86.8%. b) The proportion of variance represented by each axis within the *S. barclayi* site was the following: Axis 1, $R^2 = 0.482$; Axis 2, $R^2 = 0.187$ and Axis 3, $R^2 = 0.242$. Cumulative variation = 91.1%.

Table 1.1 Precipitation records. Precipitation during the growing season, Sitka, AK (NOAA 2005).

Year	Precipitation (mm)					
	May	June	July	Aug.	Sept.	Annual
2004	60	10	100	70	300	2451
2003	70	100	40	150	300	1740
30-yr avg.	110	80	100	160	290	2530

Table 1.2 Species dominance within each site. Average percent cover and frequency presented by community type within each site. Average cover calculated from midpoint cover class values.

Species list:	*B. glandulosa*			*S. barclayi*		
	Sedge meadow (n=3)	Closed birch fen (n=10)	Open birch fen (n=6)	Willow fen (n=8)	Sedge-forb wet meadow (n=5)	Buckbean waterway (n=3)
Trees						
Cornus stolonifera Michx.	(0)	0.3 (.2)	0.4 (.2)			
Malus fusca (Raf.)Schneid.	(0)	1.6 (.1)	(0)			
Picea sitchensis (Bong.)Carr.	0.2 (.3)	(0)	(0)			
Tall shrubs						
Betula glandulosa Michx.	(0)	68 (1.0)	21.7 (.8)			
Salix barclayi Anderss.	(0)	0.8 (.3)	(0)	31.4 (1.0)	(0)	(0)
Viburnum edule (Michx.)Raf.	(0)	0.3 (.2)	0.5 (.3)	0.1 (.1)	(0)	(0)
Low shrub						
Cornus canadensis L.	(0)	0.1 (.1)	(0)			
Ledum groenlandicum Oeder	(0)	0.5 (.2)	3.5 (.7)			
Rubus arcticus L. *stellatus* (Sm.)Boivin	6.8 (1.0)	1.3 (.6)	1.7 (.7)	0.6 (.3)	4.1 (.6)	0.8 (.3)
Forbs						
Angelica genuflexa Nutt.	2.5 (1.0)	3.3 (.8)	1.3 (.5)	5.8 (1.)	2 (.8)	(0)
Achillea millefolium L.	1.7 (.7)	2.6 (.5)	(0)			
Athyrium filix-femina (L.)Roth	(0)	1.9 (.3)	(0)			
Botrychium virginianun (L.)Sw. ssp. *europaeum* (Angstr.)Clausen	0.2 (.3)	0.1 (.2)	(0)			
Caltha leptosepala DC.	6 (.7)	1.8 (.2)	0.1 (.2)	2 (.3)	4.6 (.8)	1.7 (.7)
Aster modestus Lindl.				2.5 (1.0)	1.5 (.6)	2.5 (1.0)

Table 1.2 Continued. Species dominance within each site.

Castilleja unalaschensis (Cham.&Schlecht)Malte	5.2 (.3)	0.8 (.4)	0.1 (.2)	(0)	2.5 (1.0)	0.8 (.3)
Circaea alpina L.	(0)	0.5 (.2)	(0)			
Coptis trifolia (L.)Salisb	0.8 (.3)	(0)	(0)			
Cystopteris fragilis (L.)Bernh.	(0)	0.1 (.2)	(0)			
Dodecatheon jeffreyi Van Houtte	0.8 (.3)	(0)	6.4 (.8)			
Dodecatheon pulchellum (Raf.) Merr.				3.2 (.6)	1.5 (.6)	(0)
Epilobium glandulosum Lehm.				(0)	0.5 (.2)	(0)
Epilobium hornemannii Reichenb.				0.1 (.3)	1.1 (.6)	0.8 (.3)
Epilobium leptocarpum Hausskn.				(0)	0.5 (.2)	(0)
Equisetum fluviatile L.				0.8 (.5)	1.1 (.6)	(0)
Equisetum hyemale L.				1.9 (.9)	1.5 (.6)	0.8 (.3)
Equisteum arvense L.	2.5 (1.0)	1.8 (.7)	2.1 (.8)	2.2 (.9)	2 (.8)	2.5 (1.0)
Fritillaria camchatcensis (L.)Ker-Gawl	0.8 (.3)	0.1 (.1)	0.2 (.3)			
Galium kamtschaticum Steller ex J.A.&J.H.Schultes				0.1 (.1)	(0)	(0)
Galium trifidum L. *colombianum* (Rydb.)Hulten	(0)	0.8 (.3)	(0)			
Galium triflorum Michx.	(0)	0.8 (.3)	(0)			
Geranium erianthum DC.	2.5 (1.0)	1.8 (.7)	1.3 (.7)	0.1 (.3)	(0)	0.8 (.3)
Heracleum maximum Bartr.	(0)	2.1 (.3)	(0)			
Lysichiton americanum Hulten&St.John	(0)	11.8 (.7)	6.8 (1.0)	7.1 (.9)	3.6 (.4)	(0)
Maianthemum dilatatum (Wood)A.Ne.s.&J.F.Macbr	0.8 (.3)	0.8 (.3)	(0)			
Malaxis brachypoda (Gray)Fern	(0)	0.1 (.1)	0.1 (.2)	0.1 (.1)	0.6 (.4)	(0)
Menyanthes trifoliata L.				4.8 (.1)	3.1 (.2)	54.7 (1.0)
Oenanthe sarmentosa K.Presl ex DC.	(0)	(0)	0.4 (.2)			

Table 1.2 Continued. Species dominance within each site.

Parnassia fimbriata Koenig	0.8 (.3)	0.3 (.2)	1.8 (.8)	5.1 (.8)	1.5 (.6)	0.83 (.3)
Petasites frigidus (L.)Fries	(0)	0.3 (.1)	(0)			
Platanthera dilatata (Pursch)Lindl. Ex Beck	0.8 (.3)	0.6 (.3)	0.4 (.2)	0.8 (.5)	1.5 (.6)	0.8 (.3)
Platanthera saccata (Greene)Hult.	(0)	0.1 (.1)	(0)			
Polemonium acutiflorum Willd. Ex Roemer&J.A.Schultes	(0)	(0)	0.4 (.2)			
Pyrola asarifolia Michx. var. *purpurea* (Bunge)Fern.	0.8 (.3)	0.5 (.2)	(0)			
Sanguisorba officinalis L.	1.7 (.7)	4.6 (.8)	4.7 (1.0)	3.5 (.8)	2 (.8)	0.8 (.3)
Sanguisorba menziesii Rydb.				(0)	0.5 (.2)	(0)
Scirpus microcarpus J.&K.Presl				0.1 (.1)	(0)	(0)
Senecio triangularis Hook.	(0)	0.3 (.1)	(0)			
Stellaria sitchana Steud.	0.8 (.3)	0.8 (.4)	(0)	0.3 (.1)	0.5 (.2)	(0)
Stellaria crassifolia Ehrh.	0.8 (.3)	0.1 (.1)	(0)			
Swertia perennis L.	(0)	1.8 (.7)	4.7 (1.0)	1.3 (.5)	1.5 (.6)	0.8 (.3)
Aster subspicatus Nees	18.7 (1.0)	22.1 (1.0)	0.8 (.3)			
Tofieldia glutinosa (Michx.)Pers. *brevistyla* C.L.Hitchc.	(0)	(0)	0.1 (.2)			
Trientalis europea L. *arctica* (Fisch. ex Hook)Hult	1.7 (.7)	1.3 (.6)	0.8 (.3)	0.3 (.1)	1.5 (.6)	(0)
Viola sp.	1.7 (.7)	2.5 (1.0)	1.3 (.7)	0.9 (.4)	1 (.4)	0.8 (.3)
Graminoid						
Podagrostis aequivalvis (Trin.)Scribn.&Merr.	(0)	0.3 (.1)	(0)	(0)	1 (.4)	(0)
Agrostic exarata Trin.				(0)	0.1 (.2)	(0)
Bromus pacificus Shear				(0)	(0)	0.2 (.3)

Table 1.2 Continued. Species dominance within each site.

Calamagrostis canadensis (Michx.)Beauv.	0.8 (.3)	4.9 (.9)	0.9 (.5)	0.4 (.3)	1 (.4)	1.7 (.7)
Carex anthoxanthea J.&K. Presl	(0)	0.5 (.2)	2.6 (.2)			
Carex sitchensis Prescott	32.4 (1.0)	3.4 (.9)	6.8 (1.0)	25.1 (1.0)	29 (1.0)	6.8 (1.0)
Carex disperma Dewey	0.8 (.3)	0.6 (.3)	3.5 (.7)	0.9 (.4)	3.6 (.4)	2.5 (1.0)
Carex echinata Murr.	0.8 (.3)	(0)	1.4 (.8)	2.6 (.4)	(0)	2.5 (1.0)
Carex flava L.	0.8 (.3)	0.3 (.1)	3 (.3)	4.5 (.5)	(0)	14.3 (1.0)
Carex saxatilis L.	(0)	(0)	2.6 (.2)			
Deschampsia caespitosa (L.)Beauv.	1.7 (.7)	1.8 (.7)	1.3 (.5)	1.6 (.8)	2.1 (1.0)	0.8 (.3)
Eriophorum russeolum Fries ex Hartman				0.1 (.3)	(0)	6 (.7)
Glyceria borealis (Nash)Batchelder	(0)	0.1 (.2)	0.1 (.2)			
Hierochloe odorata (L.)Beauv.	(0)	0.3 (.1)	0.4 (.2)	1.3 (.6)	1.6 (.8)	0.8 (.3)
Trisetum cernuum Trin.	(0)	0.3 (.2)	(0)			

Table 1.3 Species richness values by community type. Mean presented with standard deviation.

***B. glandulosa* site**	
Sedge meadow (n=3)	16.3 (1.1)
Closed birch fen (n=10)	18.6 (3.1)
Open birch fen (n=6)	17.3 (4.0)
***S. barclayi* site**	
Willow fen (n=8)	15.8 (2.2)
Wet forb-sedge meadow (n=5)	16.8 (2.9)
Buckbean waterway (n=3)	13.7 (4.6)

Table 1.4 Correlation values of species in species space. Species correlations with ordination axes in species space for both sites. NA indicates that the species was not strongly correlated with any axis.

		B. glandulosa		***S. barclayi***	
Species	Species Code	Kendall's tau	Axis	Kendall's tau	Axis
Betula glandulosa	BETNAN	-0.435	2	NA	
Salix barclayi	SALBAR	NA		0.709	3
Rubus arcticus ssp. *stellatus*	RUBARCS	-0.616	3	NA	
Achilles millefolium	ACHMIL	-0.516	3	NA	
Angelica genuflexa	ANGGEN	-0.445	3	0.399	2
Aster modestus	ASTMOD	0.414	3	0.449	3
Caltha leptosepala	CALLEPH	-0.520	2	-0.578	3
Castilleja unalaschensis	CASUNA	-0.527	3	-0.692	3
Dodecatheon jeffreyi	DODJEF	-0.594	1	NA	
Dodecatheon pulchellum	DODPUL	NA		-0.401	2
Equisetum hyemale	EQUHYE	NA		0.419	2
Galium triflorum	GALTRIL	0.464	1	NA	
Geranium erianthum	GERERI	-0.428	3	NA	
Lysichiton americanum	LYSAME	0.513	3	-0.411	1
Menyanthes trifoliata	MENTRI	NA		0.719	1
Parnassia fimbriata	PARFIM	-0.551	1	NA	
Platanthera dilatata	PLADIL	NA		-0.483	3
Sanguisorba officinialis	SANOFF	NA		-0.487	1
Stellaria crassifolia	STECRA	0.427	1	NA	
Swertia perennis	SWEPER	0.564	3	-0.639	2
Aster subspicatus	ASTSUB	0.678	1	NA	
Trientalis europea	TRIEUR	-0.607	2	-0.474	3

Table 1.5 Continued. Correlation values of species in species space.

Viola sp.	VIOLA	0.491	1	-0.401	2
Calamagrostis canadensis	CALCAN	NA		-0.554	2
Carex sitchensis	CARSIT	-0.452	3	-0.471	1
Carex disperma	CARDIS	NA		0.596	1
Carex echinata	CARECHP	-0.511	1	-0.532	1
Carex flava	CARFLA	NA		0.468	1
Deschampsia caespitosa	DESCAE	NA		0.421	1

Table 1.6 Summary table of site soil-water and soil variables . Mean values with standard deviations for water variables measured for between site and between community comparisons. Values followed by different letters for site comparisons are significantly different using the Wilcoxon test ($p \leq .05$).

	site			site	
Water variables	***Betula glandulosa***	***Salix barclayi***	**Soil variables**	***Betula glandulosa***	***Salix barclayi***
Total nitrogen ($mg\,L^{-1}$)	0.67 (0.33)[a]	0.39 (0.13)[b]	Soil C:N	22.3 (12.7)	16.2 (4.5)
Total organic carbon ($mg\,L^{-1}$)	8.9 (3.4)	8.7 (3.1)	% organic matter	76.0 (18.1)	62.7 (18.2)
Total phosphorus ($\mu g\,L^{-1}$)	17.1 (16.6)	14.8 (16.5)	Soil N:P	8.2 (4.0)[a]	11.8 (2.3)[b]
Soluble Reactive Phosphorus ($\mu g\,L^{-1}$)	6.3 (6.5)	10.7 (24.4)	Soil NH_4 ($g\,m^{-3}$)	14.9 (33.4)	11.1 (12.5)
Ammonium ($\mu g\,L^{-1}$)	111.3 (110.6)	32.7 (42.3)	Soil NO_3 ($g\,m^{-3}$)	0.2 (0.2)[a]	1.0 (0.9)[b]
Nitrate ($\mu g\,L^{-1}$)	57.8 (40.2)	106.2 (97.6)	Soil P ($g\,m^{-3}$)	3.3 (11.5)	1.4 (2.1)
Sulfate ($mg\,L^{-1}$)	10.37 (13.67)	4.65 (3.05)	Soil K ($g\,m^{-3}$)	33.7 (50.5)	48.2 (36.4)
Chloride ($mg\,L^{-1}$)	2.82 (1.1)	4.8 (3.6)	Soil Ca ($g\,m^{-3}$)	3419.5 (5364.9)	4130.7 (6228.3)
Sodium ($mg\,L^{-1}$)	2.38 (0.71)	2.91 (1.47)	Soil Mg ($g\,m^{-3}$)	85.1 (50.3)	132.7 (76.0)
Potassium ($mg\,L^{-1}$)	10.2 (4.6)[a]	16.1 (3.7)[b]	Soil Fe ($g\,m^{-3}$)	105.2 (89.2)	95.0 (57.6)
Magnesium ($mg\,L^{-1}$)	0.44 (0.18)	0.59 (0.75)	Soil Al ($g\,m^{-3}$)	1.0 (1.0)[a]	0.4 (0.2)[b]
Calcium ($mg\,L^{-1}$)	41.1 (20.1)	42.5 (10.5)	Soil pH	5.9 (0.4)[a]	7.0 (0.6)[b]
Specific conductivity ($\mu S\,cm^{-1}$)	291.2 (132.2)[a]	421.3 (111.1)[b]	bulk density ($g\,m^{-3}$)	0.270 (0.128)[a]	0.262 (0.160)[b]
pH	6.3 (0.5)[a]	7.0 (0.2)[b]			
Water table (cm)	-33.0 (1.2)[a]	-20.0 (1.0)[b]			

Table 1.7 Correlation scores of environmental variables in species space. Environmental correlations with ordination axes in species space for both sites. NA indicates that the variable was not strongly correlated with any axis.

		B. glandulosa		*S. barclayi*	
Variable	**Code**	**Kendall's tau**	**Axis**	**Kendall's tau**	**Axis**
soil water					
Water table	H2O Table	-0.49	1	0.552	1
Total organic carbon	T-TOC	NA		0.400	3
Total nitrogen	W-TN	NA		-0.517	1
Total phosphorus	W-TP	-0.427	1	0.483	1
Log SRP	W-SRP	-0.575	3	.444	1
Log nitrate	W-NO3	NA		0.517	3
Log sulfate	W-SO4	0.532	1	NA	
Log ammonium	W-NH4			0.467	1
Log magnesium	W-Mg	-0.415	2	NA	
Log calcium minimum	W-Ca min	0.462	1	NA	
Log calcium maximum	W-Ca max	NA		0.433	3
Log specific conductivity	conduct	NA		0.433	3
soil nutrient					
Bulk density	Bulk density	NA		-0.667	3
Soil pH	S-pH	NA		0.500	3
Soil C:N	S-C:N	-0.509	1	NA	
Log nitrate	S-NO3	NA		-0.450	1
Log iron	S-Fe	-0.404	3	0.417	3
Log aluminum	S-Al	0.427	1	NA	
Log ammonium	S-NH4	0.474	1	NA	
Log calcium	S-Ca	NA		0.567	3
Log magnesium	S-Mg	NA		0.467	3

CHAPTER 2

Betula glandulosa – Locally restricted?

ABSTRACT

In southeastern Alaska, little is known about the disjunct population of *Betula glandulosa* and whether or not it is restricted to its current location in the Game Creek watershed. The closest known population is in the alpine zone of the Wrangell-St. Elias Mountains 150-km distant. I examined whether biotic or abiotic factors better explain *B. glandulosa* presence in a factorial field experiment that tested the effect of site and competition on germination success and seedling survival. Plots were established in two otherwise similar calcareous fens, one with and one without *B. glandulosa*. Germination success was tested in a seed scatter experiment whereas seedling survival was tested using transplants. Environmental variables were then used to assess the relationship of ecological conditions to survival. Germination rates were low (0.1%). Seedling survival was significantly higher within the birch site and higher yet without competition in the birch site. Seedling survival was not associated with any measured environmental variables. I postulate that *B. glandulosa* persistence in southeastern Alaska is dependent upon high seed rain (given the low germination success) and disturbance.

2.1 INTRODUCTION

Disjunct plant populations are distant from continuous populations within the geographical range of the species. Disjunctions can occur at different geographical scales, from smaller scales such as found in the European Alps (Schonswetter et al. 2003) to larger like those found with some Beringean species (Murray et al. 1983). Generally, there are two types of disjunctions: disjunctions that result in speciation events are "specific disjunctions," whereas disjunctions that do not produce speciation events are "intraspecific disjunctions." Disjunctions are of interest for a number of reasons. Specific disjunctions provide opportunities to study speciation events that result from adapting to different environs or from chance events (Brown and Lomolino 1998). Intraspecific disjunctions can result from historical factors such as glaciation events, and thus provide information for retracing climatic events as well as the dispersal of species (Strong and Hills 2003). Intraspecific disjunctions may also result from long-distance chance dispersal or introduction by humans where taxa persistence is linked to some key ecological factor. Lastly, disjunct populations may be useful indicators of climate change as they are found outside their normal range in stressful environments or in small patches of suitable habitat (Lennon et al. 2002).

Where we find populations disjunct from their known range, what characterizes the site? Is there an unusual set of site factors associated with the population? Is the species a strong colonizer? Or is the species' presence due to random events? Environmental conditions create habitats that dictate flora presence; however, the biotic interactions ultimately shape patterns of species' occurrence. Where abiotic conditions are stressful, we would expect the influence of biotic factors to be minimized (Grime 1979, but see Tilman 1982). In this instance, we would predict that disjunct species would persist in less than "optimal" sites as a refuge from the better-

adapted competitors. Where abiotic conditions are favorable, i.e., resource rich, we would expect competition to be a strong factor influencing species composition.

Within the Alexander Archipelago of southeastern Alaska, the Coastal Mountain Range and the Pacific Ocean create a barrier to species' dispersal. The northern region is known to house peripheral taxa at the southern limit of their known range where unusual substrates such as limestone and ultramafic geologies are present (Hultén 1968). Likewise, peripheral species at the northern limit of their known range are present in the southern region of southeastern Alaska. Calcareous fens provide unique environmental conditions, and populations on the fringe of their known range have been identified in these systems within southeastern Alaska (DeLapp 1992, McClellan et al. 2003). Calcareous fens are a subset of extremely rich fens, defined by groundwater with a high calcium concentration, circumneutral pH, high alkalinity, presence of calciphilic vegetation, and histosol soils (Almendinger and Leete 1998). The resulting hydrogeochemistry is distinct from that of the predominant bog and fen communities of the surrounding area, and, within southeastern Alaska, each island has unique species composition within these calcareous fen complexes (McClellan et al. 2003). This type of extremely rich fen is uncommon in southeastern Alaska and is rare due to the scattered presence of carbonate rock combined with the glacial history of the region. Where limestone is present the glaciomarine sediment deposition often isolates the carbonate lithology from contact with groundwater.

2.1.1 *Betula glandulosa*

The disjunct *Betula glandulosa* Michx. (dwarf or resin shrub) population was selected for study because it is found in only one documented location in the Alexander Archipelago - a calcareous fen within the Game Creek watershed on Chichagof Island in southeastern Alaska (Figure 2.1). The nearest known *B. glandulosa* populations are on the mainland near Kluane

Lake roughly 500 km northeast and in the St. Elias Mountains approximately 150 km to the northeast.

B. glandulosa is a prostrate to erect deciduous shrub species growing up to 1.5-2.5 m. in height (Groot et al. 1997). The shrub is monoecious, flowering in June with nutlet maturation in August and dispersal principally in the fall (Furlow 1997, Viereck and Little 1986). The dominant growth form in the Arctic consists of vegetative layering with adventitious roots, a response to being overgrown by moss (Hermanutz et al. 1989, Shaver and Cutler 1979). *B. glandulosa* is distributed across North America from interior Alaska south to the mountains of Colorado and California, and east to Maine, Labrador, and into Greenland (Furlow 1997, Viereck and Little 1986, Hulten 1968). *B. glandulosa* inhabits a wide variety of ecosystems, from wetlands at low elevations to upland scree slopes in the subalpine and alpine zones. This shrub is typically found where the water table remains high. The species has low nutritional requirements and prefers acidic, organic soils (Fredskild 1991, Krajina et. al. 1982). *B. glandulosa* is taxonomically similar to *Betula nana* L., and Kartesz (1999) treated *B. glandulosa* as synonymous with *B. nana*. In this study, *B. glandulosa* follows the treatment of Furlow (2000) who maintained the taxon as separate based upon leaf morphology and stature of the shrub. The range of *B. nana* extends across northwestern North America, but is not into southeastern Alaska. The species within the genus *Betula* are known to form hybrids where ranges overlap, and within North America *B. glandulosa* does form hybrids with *B. nana*, *B. neoalaskana* Sargent, *B. pumila* L., and *B. occidentalis* Hook. (Furlow 1997, Groot et al. 1997).

2.1.2 Study objectives

The objective of this study was to assess the effect of biotic and abiotic factors on the establishment of two life stages of *B. glandulosa*. If the effect of abiotic factors is significant,

then what ecological variable(s) might be related to its persistence? I first test the null hypothesis that *B. glandulosa* germination and seedling survival will be independent of site. I compare germination and survival in the absence of competition at the site where it occurs to one where it does not but which is otherwise very similar. I then evaluate the effect of competition on germination success and seedling survival. Finally, I evaluate correlations of environmental parameters to seedling survival in each site with the objective of linking persistence to some suite of ecological variables. If species' presence is controlled by abiotic conditions, then I expect *B. glandulosa* to survive with or without competition in the *B. glandulosa* site and not in the non- *B. glandulosa* site. Conversely, if biotic conditions are controlling presence and persistence then I expect the species to establish in either site without competition. Given the extremely rich character of calcareous fens, I predict that competition will have a stronger effect on germination success and seedling survival than any other key ecological factor.

2.2 METHODS

2.2.1 Geologic and hydrogeomorphic setting

The two research sites selected for study are along a Game Creek tributary (57°58'12" N, 135°26'22"W), located on Chichagof Island, a northern outer island of the Alexander Archipelago in southeastern Alaska (Figure 2.1). The Game Creek watershed is roughly 18-km long and 4-km wide at its widest point, representing the classic broad, glaciated U-shaped valley. The Kennel Creek Limestone formation is a prominent ridge roughly 1000 m in elevation on the northeast side of the Game Creek valley. The formation includes limestone with dolomite and limestone breccia, small amounts of shale and siltstone, and rare polymictic conglomerates (Karl 1996). The dominant rock type on the toeslope is calcareous graywacke with carbonate clasts,

fossil fragments, subordinate feldspar, quartz, and volcanic rock fragments. The valley bottom is comprised of glaciomarine till, the product of extensive glacial activity in the region. Calcium-rich water from this Kennel Creek marble formation discharges into the two sites located in the transition zone between the toeslope and the valley bottom.

2.2.2 Climate

Climate is typical of a perhumid rainforest with mild winters and cool summers (Alaback 1996). Mean temperatures at sea level are 10°C in the summer and 0°C in the winter, and mean annual rainfall is 254 cm (Nowacki et al. 2001). Precipitation is heaviest September into November, and the driest months are March and April. The summer of 2004 was warm with record breaking temperatures in June, July and August (NOAA 2005); additionally, a mild April caused an early "leaf-out" with robust growth in vegetation by mid-May. In conjunction with above average temperatures, precipitation records from Sitka were below normal during the growing season (May - September) (Table 1.1). Sitka is the closest station to the research site with consistent monthly data that likewise falls within the same precipitation isocline (Nowacki et al. 2001).

2.2.3 Vegetation

The predominant vegetation on the mountain slopes of Chichagof Island is Western hemlock (*Tsuga heterophylla* (Raf.) Sarg.) - Sitka spruce (*Picea sitchensis* (Bong.) Carr.) forest with Sitka alder (*Alnus viridis* (Chaix) DC. ssp. *sinuata* (Regel) A.& D. Löve) and salmonberry (*Rubus spectabilis* Pursch) forming dense thickets in the avalanche chutes. Wetlands within the transition from toeslope to valley bottom are diverse floristically. Shrub-dominated and herbaceous-dominated fens are interspersed with forested wetlands. The forested wetlands transition to Western hemlock - Sitka spruce forests on the well-drained sites along waterways

and on alluvial fans. The valley bottom is a mosaic of forested wetland and blanket bog, with open Sitka spruce stands in the riparian zone along Game Creek.

2.2.4 Site descriptions

The two research sites are along a Game Creek tributary (57°58'12" N, 135°26'22"W), located on Chichagof Island, a northern outer island of the Alexander Archipelago in southeastern Alaska (Figure 2.1). The sites selected for study are shrub fens 2-km apart within the same watershed. One site was selected due to the presence of a peripheral population of *Betula glandulosa* L. (dwarf birch), hereafter referred to as the *B. glandulosa* site. The other site was selected due to the absence of *B. glandulosa* but otherwise similar slope position, aspect and the presence of *Salix barclayi* Anderss. (Barclay's willow). This site is hereafter referred to as the *S. barclayi* site. The sites are roughly 100 m above sea level, located at the base of a massive limestone ridge. Average slope for both sites is 3% with a southwest aspect. The terracing present in both sites is likely the result of down-cutting over time from the tributary that runs perpendicular to the slope.

Within both sites, the plant communities appear to vary by terrace. The *B. glandulosa* site is dominated by *B. glandulosa* on terraces 2 and 3 (70% cover and 2.0 m height), with shrubs scattered on terrace 4 (20% cover and 1.0 m height). Terrace 1 consists of graminoids and forbs. The understory on terraces 2 and 3 is dominated by forbs, whereas the terrace 4 herbaceous layer is dominated by graminoid species. A stream flows through the site, with little containment through terrace 4 and frequent flooding across a wide swath of the area. In addition to functioning as a present disturbance source on terrace 4, this stream appears to have migrated within the site through time. The *S. barclayi* site is located on a terraced alluvial fan. The stream at this site is ephemeral, with surface flow during periods of heavy snowmelt in the spring. The

rest of the year the flow is subterranean on the backslope before discharging into the wetland. The upper two terraces of the *S. barclayi* site sit on a carbonate deposition from an apparent debris flow. The vegetation on terrace 1 is a mixture of open shrubs graminoids and forbs. Terrace 2 vegetation is dominated by shrubs, with graminoid and forb species present. Terrace 3 vegetation is comprised of sedge-forb wet meadow species. Deer browse of *S. barclayi* maintains the average shrub height at 0.5 m within this site.

2.2.5 Germination success

I tested for germination success of *B. glandulosa* seeds both with and without competition. Ten plots -- five with and five without competition located side-by-side -- were located on each terrace. I established 30 plots in each site, for a total of 60. In the plots without competition, I removed all vegetation and scored the edges to sever any roots connected with surrounding vegetation. *B. glandulosa* seeds were collected on site in May of 2003 and 2004. I scattered one hundred seeds in each 15 cm x 15 cm plot in July of 2003, and fifty seeds in each plot in May of 2004. Germination success was measured at the end of the growing season (late August 2003 and early September 2004). No plots were established in terrace 4 of the *S. barclayi* and *B. glandulosa* sites due to the surface flow of water at the time of seeding.

2.2.6 Seedling survival

I collected *B. glandulosa* seeds from the Game Creek site in the spring of 2003 and grew them in a greenhouse on Mitkof Island for three months prior to transplanting them into the *B. glandulosa* and *S. barclayi* sites. I transplanted thirty seedlings into the *S. barclayi* site and 40 into the *B. glandulosa* site in late August of 2003 (one seedling per plot, ten plots per terrace). The additional ten plots were located in terrace 4 of the *B. glandulosa* site. No seedlings were transplanted into the ponded terrace 4 of the *S. barclayi* site. Again, I tested for seedling survival

both with and without competition in 30 cm x 30 cm plots positioned side-by-side. I removed all vegetation and scored the border of the plots testing survival without competition. Prior to transplanting the seedlings, I quantified seedling height, number, and length of leaves to analyze whether or not seedling vigor was a covariate in seedling survival. I measured survival in early September of 2004.

2.2.7 Environmental variables

Plot center for the soil and water sampling was 1 m from the germination and seedling treatments. Methodology for the soil and water sampling is detailed in Chapter 1. I measured the water table through the course of the growing season using pressure transducers (Global Water, Inc.). A suite of water chemistry variables was collected every other month, with the results pooled by plot for exploratory analysis. Parameters included: pH, conductivity, total carbon, nitrogen and phosphorus, nitrate, ammonium, soluble reactive phosphorus (SRP), total organic carbon (TOC), base cations, sulfate, and chloride. I collected soil samples at 25-cm depth in July. Physicochemical descriptors included bulk density, pH, percent organic matter, percent total carbon, nitrogen and phosphorus, nitrate, ammonium, orthophosphate, base cations, aluminum, and iron.

2.2.8 Data analysis

I tested the effect of site (*S. barclayi* or *B. glandulosa*) and competition (with or without) on percent *B. glandulosa* germination using two-way analysis of variance (PROC GLM). I used logistic regression to evaluate the probability of survival, including the vigor covariates in the model (PROC LOGIST). Environmental variables were then fit in a model with site and competition using Akaike's selection criterion to determine the best fit. All continuous environmental variables were $\log_{10}$ transformed for normalization of the variances. Terraces were

also included in the model to tease out within site differences in survival. Due to the n=3 sample size on terrace 3 of the *S. barclayi* site and terrace 1 of the *B. glandulosa* site for the descriptive portion of this study, I used environmental variable averages by terrace for eight of the plots in the analysis. All statistical analyses were completed using SAS software (SAS Institute, Inc., version 9.1 2002). Analysis of environmental parameters was not done with germination success due to the extremely low germination rates.

2.3 RESULTS

2.3.1 Germination success

Out of 9000 seeds scattered, only 12 germinated and survived to the age of three months (9 of 6000 in 2003, 3 of 3000 in 2004). In 2004, the effect of site, competition, or the interaction of site and competition upon germination was not statistically significant ($F_{(3,56)}$=1.28, P=0.29), but it should be noted that all three of the seeds that germinated and survived were at the *S. barclayi* site. Again, none of the independent variables were significant in 2003 ($F_{(3,56)}$=1.72, P=0.17); however, eight of the nine seeds germinating were without competition and fairly evenly distributed between the two sites (Table 2.2).

2.3.2 Seedling survival

Seedling survival was dependent upon site and the site by competition interaction (X^2=14.77, df=6, P=0.002). Survival was higher within the *B. glandulosa* site, and higher yet again without competition in the *B. glandulosa* site (Table 2.3, Figure 2.2). None of the covariates explained a significant proportion of the variation; therefore, the health and size of the seedling apparently had no effect on the survival outcome. Seedling survival was not

significantly influenced by terraces. Soil percent carbon was the only significant environmental variable, with lower percentages present with surviving seedlings (X^2=16.23, df=7, P=0.004).

2.4 DISCUSSION

2.4.1 Survival - Game Creek

B. glandulosa establishment from seed was exceedingly low (0.1%, Figure 2.2) and does not suggest that this species is a strong colonizer. Germination success may have been impacted by any number of factors, including desiccation in the open plots, quality of the seed collected, and transport of the seed out of the plots by surface water flow during rain events. However, given the lack of *B. glandulosa* seedlings observed during field sampling, the germination rates found are likely reflective of what is occurring within the *B. glandulosa* site. Apart from the low germination rate at this site, the shrub does exhibit characteristics of a pioneer species elsewhere: seed production is copious where individuals are numerous and conditions are not stressful (pers. obs.); germination rates have been observed at 60% under controlled environs in Quebec (De Groot et al. 1997), and *B. glandulosa* has been found to be a colonizer of disturbed sites in northern Canada (Weis and Hermanutz 1993). With copious seed production within the *B. glandulosa* site and high germination rates found in other sites, a 0.001% germination rate would not necessarily preclude *B. glandulosa* establishment. This points to factors other than seed quantity and quality as responsible for the low germination rates found over two years in the Game Creek sites.

Unlike germination rates, survival rates were high: 54% of the seedlings survived. Seedling survival within the *B. glandulosa* site (60%, Figure 2.2) was twice that of the seedlings

within the similar site where the species is absent (30%). Thus it appears that the *B. glandulosa* site is particularly favorable for this species. Furthermore, within the *B. glandulosa* site, survival in the absence of competition was high (85%) and greatly reduced in the presence of competitors (to 35%). This indicates that the favorable site abiotic conditions are overridden by strong competition effects; therefore the role of disturbance, such as the migrating stream within the *B. glandulosa* site, may play a major role in seedling survival (Fynn et al. 2005, Gaudet and Keddy 1995). The absence of similar significant competition effects in the *S. barclayi* site further points toward other factors associated with seedling survival. Light was not measured in this study, and it may be a primary limiting resource affecting seedling survival.

Within site and competition treatments, neither the terraces nor the environmental variables explained seedling survival; therefore, no germination and/or establishment appear associated with germination and/or establishment. This suggests that I missed some environmental variable(s) linked with the persistence of this shrub due to parameter selection or small sample size and the high variability of the parameters measured. Conversely, the disturbance regime and light may be more important for the establishment of *B. glandulosa* seedlings than the suite of below ground environmental variables measured. The comparison between the two calcareous fens captured a narrow range of environmental variables on the nutrient rich end of the wetland spectrum, and does not allow us to generalize about the prediction of competition as a strong factor influencing species composition where abiotic conditions are favorable. The two sites sampled do differ from the more nutrient poor environs described in the literature for *B. glandulosa* community types (Fredskild 1991, Karjina et al. 1982, MacKenzie and Moran 2004, Slack et al. 1980, Viereck et al. 1992). A range of wetland

types across the poor to rich gradient needs to be sampled within southeast Alaska if we are to determine if this shrub is physiologically constrained to more nutrient rich sites in the region.

2.5 CONCLUSIONS AND DIRECTIONS FOR FUTURE RESEARCH

B. glandulosa germination rates were low regardless of site and competition. *B. glandulosa* seedlings fared much better within the *B. glandulosa* site when evaluating the effect of site on survival. I predicted that if biotic conditions are controlling then we may expect the species to establish in either site without competition; however, this was only realized in the *B. glandulosa* site. I conclude that abiotic factors are important in seedling survival, and that competition plays a major role. I postulate that *B. glandulosa* persistence is dependent upon high seed rain (given the low germination success) and disturbance. Studies investigating seed rain would help determine the likelihood of long-distance transport in the area, and seed bank studies would assess the long-term viability of seeds. Furthermore, the competitive ability of *B. glandulosa* in disturbed sites could be tested against regionally adapted vegetation.

REFERENCES

Alaback, P. B. 1996. Biodiversity patterns in relation to climate: the Coastal Temperate Rainforests of North America. In *High-latitude Rainforests and Associated Ecosystems of the West Coast of the Americas*. R.G. Lawford, P.B. Alaback and E. Fuentes eds. Springer-Verlag, Inc., New York, NY, USA.

Almendinger, J. E. and J. H. Leete. 1998. Peat characteristics and groundwater geochemistry of calcareous fens in the Minnesota River Basin, U.S.A. Biogeochemistry 43:17-41.

Brown, J. H. and M. V. Lomolino. 1998. *Biogeography*, 2nd ed. Sinauer Associates, Sunderland, MA.

De Groot, W. J., P. A. Thomas and R.W. Wein. 1997. *Betula nana* L. and *Betula glandulosa* Michx. Journal of Ecology 85:241-264.

Drexler, J. Z. and B. L. Bedford. 2002. Pathways of nutrient loading and impacts on plant diversity in a New York peatland. Wetlands 22:263-281.

Fredskild, B. 1991. The genus *Betula* in Greenland – Holocene history, present distribution and synecology. Nordic Journal of Botany 11:393-412.

Furlow, J. J. 1997. Betulaceae. Flora of North America Editorial Committee, eds., *In Flora of North America* Vol. 3, Oxford University Press, New York, NY.

Fynn, R. W. S., C. D. Morris and K. P. Kirkman. 2005. Plant strategies and trait trade-offs influence trends in competitive ability along gradients of soil fertility and disturbance. Journal of Ecology 25:239-251.

Gaudet, C. L. and P. A. Keddy. 1995. Competitive performance and species distribution in shoreline plant communities: A comparative approach. Ecology 76:280-291.

Grime, J. P. 1979. *Plant strategies and vegetation processes*. James Wiley, NY, USA.

Hermanutz, L. A., D. J. Innes and I. M Weis. 1989. Clonal structure of arctic dwarf birch (*Betula glandulosa*) at its northern limit. American Journal of Botany 76:755-761.

Hultén, E. 1968. *Flora of Alaska and Neighboring Territories*. Stanford University Press, Stanford, CA, USA

Karl, S. 1996. Preliminary geologic map of northeastern Chichagof Island, Alaska. Open File report 96-53. U.S. Geological Service, Denver, CO, USA.

Kartesz J. T. 1999. A synonymized checklist and atlas with biological attributes for the vascular flora of the United States, Canada, and Greenland. In: Kartesz JT, Meacham CA. Synthesis of the North American Flora, Version 1.0. Chapel Hill: North Carolina Botanical Garden.

Krajina, V. J., K. Klinka and J. Worrall. 1982. Distribution and ecological characteristics of trees and shrubs of British Columbia. Vancouver: Faculty of Forestry, University of British Columbia.

Lennon, J. L., W. E. Kunin, S. Corne, S. Carver and W. W. S. Van Hees. 2002. Are Alaskan trees found in locally more favourable sites in marginal areas? Global Ecology and Biogeography 11:103-114.

MacKenzie, W. H. and J. R. Moran. 2004. Wetlands of British Columbia: a guide to identification. Land Management Handbook No. 52. Research Branch, British Columbia Ministry of Forestry, Victoria, B.C., Canada.

McClellan, M. H., T. Brock and J. F. Baichtal. 2003. Calcareous fens in southeast Alaska. PNW-RN-536. USDA Forest Service, Pacific Northwest Research Station, Juneau, AK, USA.

Murray, D. F., B. M. Murray, B. A. Yurtsev and R. Howenstein. 1983. Biogeographic significance of steppe vegetation in subarctic Alaska. Permafrost: Fourth International Conference, Proceedings 4:883-888.

National Oceanic and Atmospheric Association. 2005. http://www4.ncdc.noaa.gov/cgi-win. (accessed 12/2005).

Nowacki, G., M. Shephard, P. Krosse, W. Pawuk, G. Fisher, J. Baichtal, D. Brew and E. Kissinger. 2001. Ecological Subsections of Southeast Alaska and Neighboring Areas of Canada. R10-TP-75. USDA Forest Service, Alaska Region, Anchorage, AK, USA.

Ritchie, J. C. 1974. Modern pollen assemblages near the arctic tree line, Mackenzie Delta region, Northwest Territories. Canadian Journal of Botany 62:381-396.

SAS Institute, Inc. 2002. SAS Version 9.1. SAS Institute, Inc. Cary, NC, USA.

Schonswetter, P. A. Tribsch, G. M Schneeweiss and H. Niklfeld. 2003. Disjunctions in relict alpine plants: phylogeography of *Androsace brevis* and *A. wulfeniana* (Primulaceae). Botanical Journal of the Linnean Society 141:437-446.

Shaver, G. R. and J. C. Cutler. 1979. The vertical distribution of live vascular phytomass in cottongrass tussock tundra. Arctic and Alpine Research, 11:335-342.

Strong, W. L. and L. V. Hills. 2003. Post-hypsithermal plant disjunctions in western Alberta, Canada. Journal of Biogeography 30:419-430.

Tilman, D. 1982. Resource competition and community structure. Princeton University Press, Princeton, NJ, USA.

Viereck, L. A., C. T. Dyrness, A. R. Batten and K. J. Wenzlick. 1992. The Alaska Vegetation Classification. General Technical Report PNW-GTR-286. USDA Forest Service Pacific Northwest Research Station, Portland, OR, USA.

Viereck, L.A. and E. L. Little, Jr. 1986. Alaska Trees and Shrubs. University of Alaska Press: Fairbanks. pp. 130-132.

Weis, I. M. and L. A. Hermanutz. 1993. Pollination dynamics of arctic dwarf birch (*Betula glandulosa*; Betulaceae) and its role in the loss of seed production. American Journal of Botany 80:1021-1027.

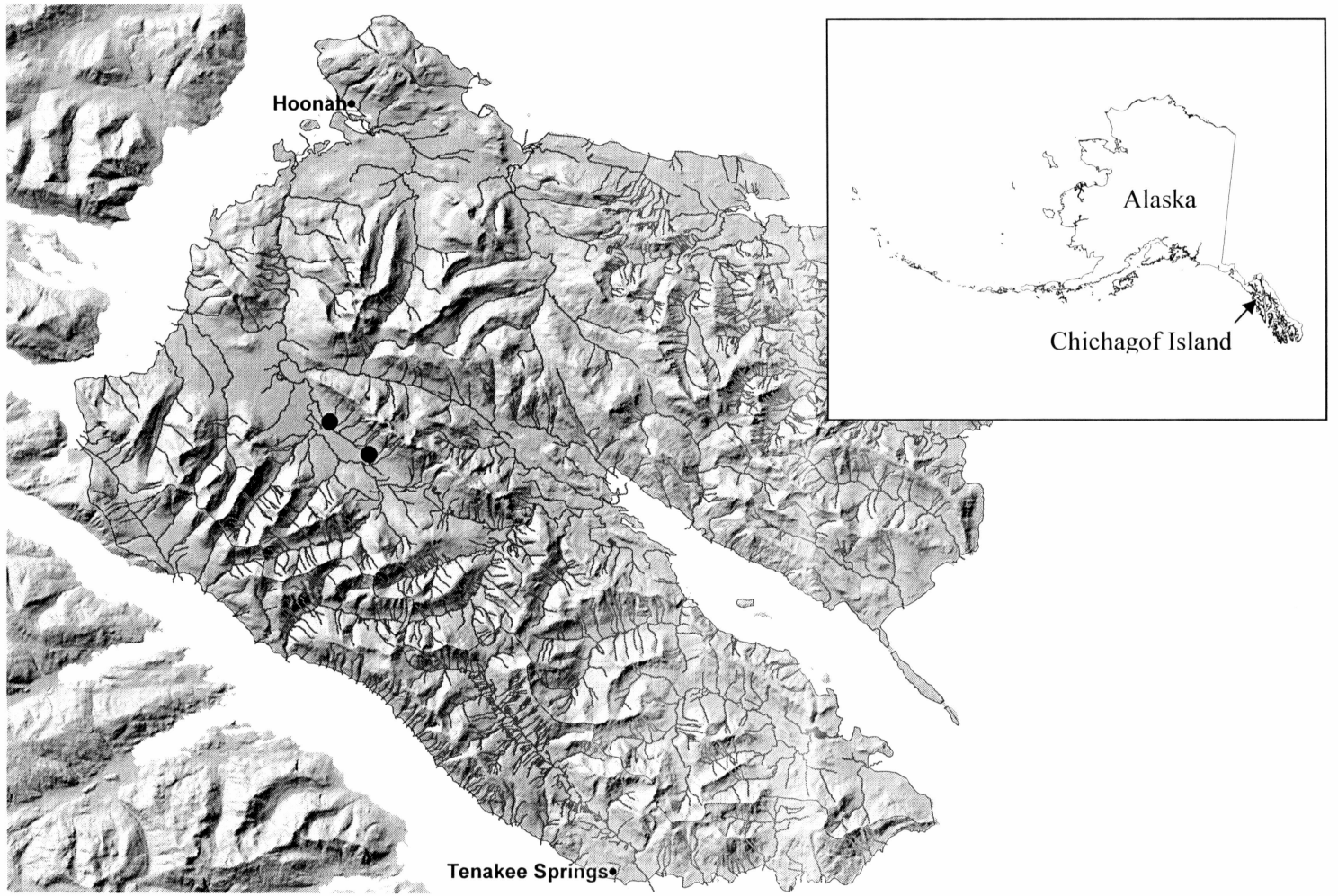

Figure 2.1 Research sites in the Game Creek watershed, Chichagof Island.

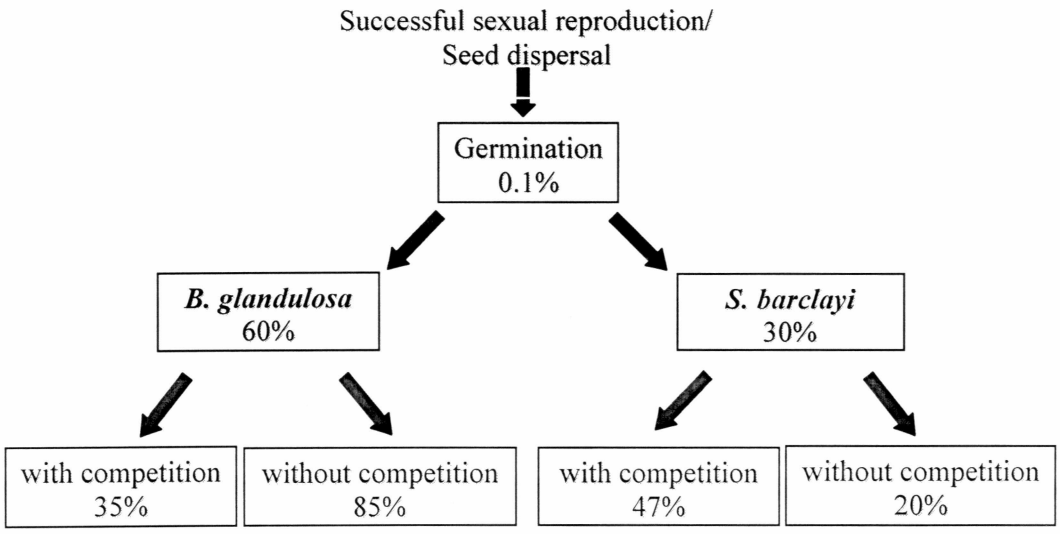

Figure 2.2 Diagram depicting survival in the two *B. glandulosa* life phases. Diagram depicting establishment success of two life phases of *B. glandulosa* in two different sites as well as with and without competition. Numbers are percent survival for transplanted seedlings and percent germination for seeds scattered.

Table 2.1 Precipitation during the growing season. Precipitation during the growing season, Sitka, AK (NOAA 2005).

Year	Precipitation (mm)					
	May	June	July	Aug.	Sept.	Annual
2004	60	10	100	70	300	2451
2003	70	100	40	150	300	1740
30-yr avg.	110	80	100	160	290	2530

Table 2.2 Percent germination success in 2003 and 2004. Site, competition, and site x competition.

		2003	
	Competition total	B. glandulosa	S. barclayi
Site total		0.27%	0.33%
With competition	0.03%	0.07%	0%
Without competition	0.27%	0.20%	0.33%
		2004	
		B. glandulosa	S. barclayi
Site total		0%	0.20%
With competition	0.07%	0%	0.07%
Without competition	0.13%	0%	0.13%

Table 2.3 *B. glandulosa* seedling survival. Logistic regression of site, competition and site x competition effects upon seedling survival.

Source of variation	df	Wald X^2	P
number	1	0.4654	0.4951
length	1	0.1344	0.7139
height	1	1.0608	0.303
competition	1	0.2837	0.5943
site	1	3.9378	0.0472
competition x site	1	6.8844	0.0087

Note: Number, length and height were used as the covariates.

GENERAL CONCLUSIONS AND DIRECTIONS FOR FUTURE RESEARCH

My study was the first to describe two calcareous fens in detail within the coastal western hemlock biogeoclimatic zone. This work contributes to our picture of rare plant communities and will improve both our understanding of the distribution of rare and uncommon plant populations and our ability to preserve these unique wetland systems. Additional work is needed to identify other calcareous fen communities across the Alexander Archipelago to capture the diversity of these rare plant communities. I show that in this perhumid region, species patterns within calcareous fens are most strongly influenced by water table and less so by soil and water chemistry. The sampling that occurred during this study had decent spatial coverage, but did not have the temporal coverage to produce clear differences between the vegetation assemblages. Further work would be required to tease out the influence of water chemistry upon plant composition. Such work might allow us to better manage the landscapes that these communities lie within to avoid disrupting the unique settings that produce calcareous fens in southeastern Alaska.

The presence of the disjunct *B. glandulosa* population is likely the result of a chance dispersal event from a source on the northeastern side of the Coastal Mountain Range. *B. glandulosa* germination rates were low regardless of site and competition. *B. glandulosa* seedlings fared much better within the *B. glandulosa* site when evaluating the effect of site on survival. I predicted that if biotic conditions are controlling then I may expect the species to establish in either site without competition; however, this was only realized in the *B. glandulosa* site. I conclude that abiotic factors are important in seedling survival, and that competition plays a major role. I postulate that persistence of *B. glandulosa* persistence is dependent upon high seed rain (given the low germination success) and disturbance. Studies investigating seed rain would help determine the likelihood of long-distance transport in the area, and seed bank studies

would assess the long-term viability of seeds. Furthermore, the competitive ability of *B. glandulosa* in disturbed sites could be tested against better-adapted vegetation.